

CONTRIBUTIONS
of the
HAWAII MARINE LABORATORY
UNIVERSITY OF HAWAII
For the Year 1956



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44. [Hiatt, Robert W. In press. Factors influencing the distribution of corals on the reefs of Arno Atoll, Marshall Islands. 8th Pacific Sci. Congress Proc.]
- 45-46. Distributed in 1954.
- 47-48. Distributed in 1955.
49. [Gosline, W. A. In press. Nature and evolution of the Hawaiian inshore fish fauna. 8th Pacific Sci. Congress Proc.]
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Beachrock in the Hawaiian Islands¹

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Reprinted from PACIFIC SCIENCE
October, 1956

Beachrock in the Hawaiian Islands¹

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BEACHROCK is a stratified calcareous sandstone (calcareenite) or conglomerate (calcirudite) occurring along many beaches that are composed of shells or other calcareous debris. It is common on beaches of islands that are bordered by coral reefs. Although many authors have described beachrock, few have agreed on its origin, either because critical data are lacking or because beachrock may form in several different ways. Preliminary studies of beachrock in the Marshall, Mariana, and Hawaiian Islands led the authors to believe that detailed mapping of beachrock in the Hawaiian Islands might show whether the distribution is related to abundance and composition of ground water or to other factors of the shore environment.

Examination of the shores of Oahu, Kauai, Molokai, and Maui during parts of June and July, 1954, was made possible by funds from Office of Naval Research contract NR 081-217.

Aid in field mapping, discussion, and critical reading of the manuscript was kindly given by Dr. Douglas Inman of Scripps Institution of Oceanography. Dr. Harold S. Palmer of Honolulu also read the manuscript and made some valuable suggestions.

GENERAL DESCRIPTION

Composition

The material that becomes cemented into beachrock is beach sand or gravel, chiefly

calcareous. The sand ranges from fine to very coarse and, like other beach sands, is very well sorted (Table 1). Its generally coarse grain size, excellent sorting, and high degree of rounding, make it very permeable. Tests on progressively coarser Oahu samples 14, 2, and 4 of Table 1, yielded permeabilities of 37, 120, and 570 darcys, respectively, values that are comparable with those of other beach sands.

The grains of sand consist chiefly of broken and worn pieces of calcareous parts of organisms, plus minor amounts of volcanic detritus. Volcanic detritus is unusually abundant in beachrock at Ohikilolo (about 2 miles south of Makua) on Oahu where it forms thin brown laminae, and at Kekaha on Kauai where it makes up the bulk of the beachrock as it does also of the unconsolidated sand. Generally, however, the volcanic detritus comprises only a small percentage of the total grains. A summary of the composition of 33 samples of loose beach sand is given in Table 1. The source organisms were identified by shape and mineralogy of the grains: Foraminifera and calcareous red algae being calcite; *Halimeda* and madreporarian coral being aragonite. The mineral form was determined by use of a solution of cobalt nitrate (Meigen's solution) which stains aragonite violet and does not affect calcite. Some pelecypod and gastropod shells consist of both aragonite and calcite; thus some become stained and others are not affected. Accordingly, shells were identified only by remnants of flat or curved surfaces and occasionally by traces of decorative colors. These methods are more fully described in a report on sediments of Guam (Emery, in manuscript). Comparison of the composition of beach sands of the Hawaiian

¹ Contribution of Allan Hancock Foundation No. 167; contribution of Hawaii Marine Laboratory No. 76; published with the permission of the Director as paper No. 38 in the journal series of the Hawaiian Sugar Planters' Association. Manuscript received February 3, 1956.

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Islands, Guam, and Bikini (Emery, Tracey, and Ladd, 1954: 38) shows the same major constituents in all the sands, but some differences in their relative proportions (Table 1). In the Hawaiian beach sands the most abundant constituent appears to be fragments of pelecypod and gastropod shells. Pieces of calcitic debris believed to be from calcareous red algae are next, followed closely by tests of Foraminifera, mainly *Amphistegina* with occasional *Marginopora*. Coral is relatively rare, and *Halimeda* debris was not found. The remaining material, called "fine debris" was too minute to permit visual identification of source organisms. Examination of polished sections of beachrock after similar staining showed the same assemblage of organisms, but percentage determinations were hampered by the presence of much calcitic cementing material.

Gravels that become cemented into beach conglomerate consist of wave-worn coral heads, large mollusk shells, pieces of basalt (Fig. 1), and reworked slabs of older beachrock (Fig. 2). Among the few places where beachrock contains volcanic gravels are areas near Kaena Point, Hauula, and Kapoho Point on Oahu, and Laau Point on Molokai. Silt and clay may also be present in beachrock



FIG. 2. Beachrock at Keaau, Oahu, containing reworked slabs of older beachrock.

but are most conspicuous as distinct interbedded layers of alluvium or soil as at Keaau on Oahu (Fig. 3).

Near Laniloa Point and Kapoho Point on Oahu, and Nohili on Kauai, eolianite overlies beachrock near the high tide level. It may be distinguished by its finer grain size, steeper dip, and generally poorer cementation.

Cementation

The cementing material that binds sand into beachrock has been described by Ginsburg (1953), Emery, Tracey, and Ladd (1954: 43–45, 148, 149, pls. 22, 50, 52, 58), Illing (1954: 48, 70), and Ranson (1955) as consisting of calcite with some aragonite. Cementing material in beachrock from the Hawaiian Islands is similar to that described elsewhere, except that no aragonite was found. Failure of any of the pore fillings to become stained with Meigen solution indicates that all of it is calcite. Dr. Heinz Lowenstam of California Institute of Technology kindly confirmed the determination using a different stain.

Thin sections of beachrock from the site of Figure 4 show that pores of the upper layers are more completely filled than those of the lower layers (Table 2). Rinds, 30 to 60 μ thick and consisting of clear acicular calcite crystals about 4 μ thick, surround all the grains in the



FIG. 1. Beachrock 3½ miles east of Kaena Point, Oahu. Lower layers contain many cobbles of volcanic rock

loose slab, surround less than 1 per cent of the grains in Layer G, and are absent in lower layers. The rest of the pore filling is brown calcite having randomly oriented grains that are more or less equidimensional and about $2\ \mu$ in diameter. If the pore filling found in the loose slab has passed through the stages of cementation represented by the lower layers, A to C, the rind of acicular calcite must be a secondary recrystallization feature.

The more complete filling of pores near the surface correlates with the common observation that beachrock is much harder at its exposed surface than at a depth of only an inch or two. An evaluation of the degree of cementation of beachrock at depth was made in the bay just west of Kahuku Point on Oahu. In this area, beachrock is especially well exposed (Fig. 4) because of retreat of the beach, probably due largely to sand removal by man. At least seven distinct layers of

beachrock are present, some of which contain slabs reworked from older layers. Inspection of the exposed portions showed that the lower layers are less well cemented than the upper ones. The hardness of each layer was determined semiquantitatively by measuring the depth that a drill rod could be driven by 50 blows of a 16-pound sledge hammer (Fig. 5). Each layer was found to be slightly harder at its top surface than at depth. A deep hole, starting in Layer G, showed variations in driving rate correlative with the variations measured at the surface for the respective layers. The lesser resistance to driving found at depth also correlates with layers of poor cementation as judged from outcropping edges. Increased resistance at the bottom of the hole was probably due to entry into underlying reef rock. Similar results were obtained in another deep hole started in Layer C. Decrease in cementation at depth is also



FIG. 3. Whaleback of beachrock at Keaau, Oahu, with two interbedded layers of red alluvium.



FIG. 4. Layered beachrock dipping seaward at west side of small bay west of Kahuku Point, Oahu. Note reef rock on left against which beachrock abuts. Site of measurements diagrammed in Figure 5 is at left center.

well shown in the walls of a large drainage ditch cut through 5 feet of beachrock at Waieli on Kauai.

The characteristically poorer cementation at depth leads to ease of undercutting and movement of large slabs by waves. A slab near Kahuku Point on Oahu weighing probably 15 tons may have been overturned by the tsunami of 1946 (Fig. 6). Solution basins have just begun to form on the exposed bottom. Other areas having numerous loose slabs are Barbers Point, the beach a mile south of Waianae, and Makua on Oahu; Nohili on Kauai; and Hale o Lono on Molokai. At Nohili, erosion of soft material from beneath beachrock has allowed large slabs to slump to a position several feet below low tide level. The loose slabs are generally much harder than beachrock *in situ*, probably because cementation has proceeded from both top and bottom. When struck with a hammer the most firmly cemented slabs ring like gongs.

Surface

The surface of poorly cemented beachrock is rough, granular, and friable. That of well-

cemented beachrock, however, is hard and becomes modified by at least four separate processes: polishing and film formation, discoloration by boring blue-green algae, biochemical solution, and abrasion.

Polishing of the surface is fairly common. In part, it is produced by continual washing of sheets of calcareous sand across the rock. It is present, therefore, chiefly where thin patchy sands overlie the beachrock. Cross sections of truncated shells, coral and other recognizable organic debris show on the surface. Polishing is supplemented by deposition of a film of very thinly laminated aragonite on the surface, which, as at Bikini (Emery, Tracey, and Ladd, 1954: 46, pls. 42, 43), fluoresces a bright reddish-orange under ultraviolet light. The film is especially well shown on beachrock at Nanakuli and on basalt at Mauna Lahilahi (about 1½ miles southeast of Makaha) on Oahu, on beachrock at Nohili on Kauai, and on beachrock at Kepuhi on Molokai. Especially at Nanakuli (Fig. 7) and Nohili the film appears to constitute a form of case-hardening that resists the development

of solution basins. Some of the loose sands, such as Oahu sample 4 and Maui sample 1 of Table 1, are also highly polished and contain many grains which fluoresce. Illing (1954: 69) has noted similarly polished and coated sand grains on Bahaman beaches.

The second process that modifies the surface of hard beachrock is a darkening that is produced by activities of boring blue-green algae. In general the rock surface is a dull medium-to-dark gray, but at a few sites it is bright blue. Among the latter sites are Kawela Bay, Barbers Point, and Nanakuli on Oahu, and Kepuhi on Molokai. A piece of coral embedded in beachrock at Barbers Point

was examined by Dr. Maxwell S. Doty of the University of Hawaii, who found *Entophysalis crustacea* and *Galothrix* living at the surface. For $\frac{1}{4}$ inch beneath the surface there was a succession of colored bands that Doty ascribed to natural chromatography of plant pigments and their decomposition products. The bands and their probable composition are as follows, from the surface inward:

blue—phycocynin
pink—phycoerythrin
clear
yellow—a carotinoid
green (thickest)—chlorophyll

Small pink or green spots at the sides of

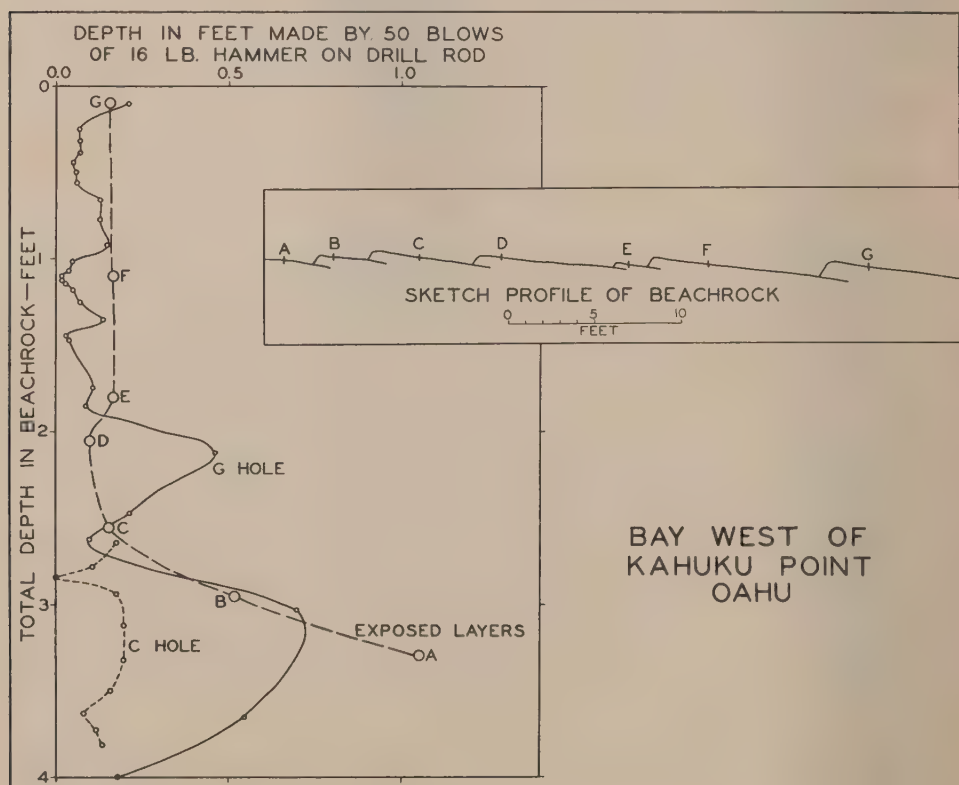


FIG. 5. Semiquantitative measurement of rock hardness, or degree of cementation, as determined by depth to which a drill rod could be driven by 50 blows of a sledge hammer. Line with long dashes shows measurements for exposed edges of layers. Solid line shows variation of hardness with depth in a hole driven vertically through all layers. Line with short dashes shows variation in a hole through three lowest layers.

LOCATION	MEDIAN DIAMETER MM.	SORTING COEFFICIENT	RESIDUE INSOLUBLE IN DILUTE HCl PER CENT BY WEIGHT	COMPOSITION OF CALCAREOUS PORTION (Per cent by Weight)				
				Foram- inifera	Shells	Fine debris	Halimeda debris	Coral
Oahu								
1. 5 mi. E Kaena Pt.....	0.56	1.16	30	15	30	0	0	25
2. 1½ mi. W Mokuieia.....	0.98	1.29	5	25	35	0	0	10
3. Waimea Bay.....	0.73	1.33	5	40	40	0	0	5
4. 1 mi. E Waimea.....	2.10	1.50	0	2	55	0	0	5
5. ½ mi. S Laniloa Pt.....	0.38	1.44	5	5	40	20	0	5
6. E side Kualoa Pt.....	0.56	1.32	2	10	35	0	0	5
7. N Kaneohe Bay.....	0.18	1.69	99					
8. ¼ mi. N Kapoho Pt.....	0.67	1.31	8	35	35	0	0	5
9. Kailua.....	0.58	1.54	1	15	30	0	0	5
10. 1 mi. S Kailua.....	0.22	1.22	45	10	25	50	0	5
11. Waimanalo.....	0.31	1.13	1	20	40	10	0	10
12. Hanauma Bay (E Koko Head).....	0.63	1.47	98					
13. 2 mi. NW Koko Head.....	0.34	1.33	2	10	35	10	0	5
14. S side Diamond Head.....	0.62	1.29	30	10	30	0	0	20
15. W Ewa Beach.....	0.83	1.73	5	15	35	0	0	5
16. ½ mi. N Nanakuli.....	0.58	1.45	2	30	25	0	0	5
17. 1 mi. S Makaha.....	0.55	1.70	1	60	25	0	0	0
Kauai								
1. Haena.....	1.30		5	60	20	0	0	0
2. Hanalei Bay.....	0.20	1.53	80					
3. Kapaa.....	0.58	1.36	1	1	20	0	0	20
4. 3 mi. SE Waieli.....	0.28	1.43	0	5	15	0	0	25
5. Waieli.....	0.22	1.35	0	5	40	0	0	20
6. 4 mi. NE Nohili.....	0.40	1.30	10	5	15	0	0	35
Molokai								
1. 2 mi. S Kepuhi.....	0.45	1.19	5	50	20	0	0	0
2. Halawa.....	0.29	1.22	70	40	45	0	0	5
3. 5 mi. SW Cape Halawa.....	0.18	1.21	97					
4. 4 mi. E Kaunakakai.....	0.37	1.23	90	10	45	0	0	5
5. 1 mi. W Kaunakakai.....	0.23	1.61	75	10	65	0	0	10
Maui								
1. 2 mi. S Makena.....	0.41	1.50	1	60	20	5	0	0
2. 5 mi. S Kihei.....	0.19	1.16	10	10	40	40	0	0
3. 5 mi. SE Lahaina.....	0.23	1.20	95					
4. 2 mi. N Honokowai.....	0.76	1.49	40	50	35	0	0	0
5. Lower Paia.....	1.10		5	5	20	10	0	25
Hawaiian Islands average (33).....	0.54	1.38	29	21	33	5	0	9
Guam average (11).....	0.45	1.41	9	8	29	2	6	36
Bikini average (30).....	0.87	1.51	0	26	9	4	2	28

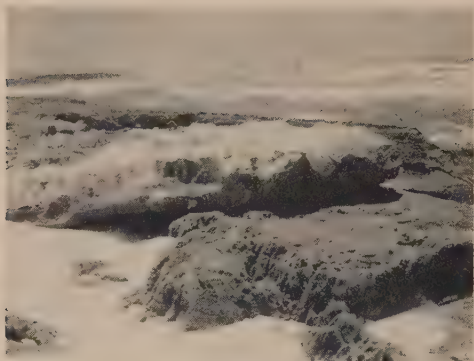


FIG. 6. Large overturned slab of beachrock $\frac{1}{2}$ mile east of Kahuku Point, Oahu, estimated to weigh about 15 tons. Solution basins have begun to form on the now exposed bottom.

boulders and in some solution basins are evidently the result of natural removal of the original, outer, colored layers. A brief description of these algae and their effect in coloring the surface of limestone has been given by Newhouse (1954). As pointed out by Cloud (1952: 28, 29) blue-green algae also invade the surface layer of loose beach sand, where they make a thin green layer and provide a weak form of cementation.

The remaining two surface processes, solution and abrasion, develop larger erosional features that have been well described by Wentworth (1944). Most common are basins

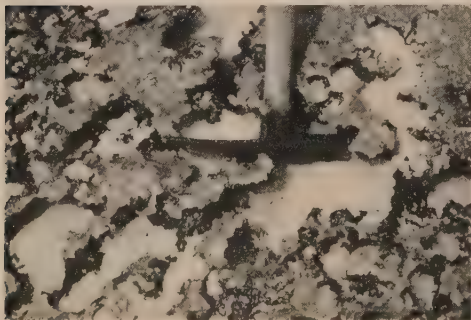


FIG. 7. Solution basins in beachrock having a case-hardened surface formed by deposition of a thin film of calcium carbonate at a place $\frac{1}{2}$ mile north of Nanakuli, Oahu.

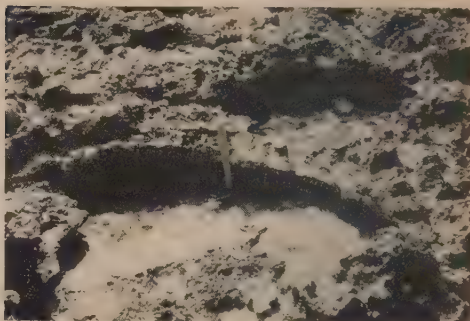


FIG. 8. Solution basins in reef rock $\frac{1}{2}$ mile north of Mauna Lahilahi, Oahu. The reef rock surface is seen to be typically rougher than that of beachrock.

produced through solution of calcium carbonate by sea water trapped in pools (Fig. 8). This process is a complicated one and, as it is described rather fully by Revelle and Emery (in press), it will not be discussed here except to point out that solution basins are best developed and have sharp serrated edges in well-cemented beachrock (Layer G of Fig. 5, for example), they have rounded edges in moderately cemented beachrock (Layer F), and they do not exist in poorly cemented beachrock (Layers A to E). Their absence in poorly cemented beachrock is the result of high permeability that allows the pools to drain before much solution can occur. Solution also has produced water-level terraces that usually are divided by narrow low ridges into a series of rimmed pools (Fig. 9). These terraces and rimmed pools are common in reef rock of all the islands (Wentworth, 1939) but were noted in beachrock only at Nohili on Kauai, and at Hale o Lono on Molokai.

In contrast to the roughly circular form of solution basins, there are channels that are elongate and extend down the slope of the beachrock. These features have smooth, straight sides, and they quite evidently are produced by mechanical erosion along joints or other discontinuities through movement of sand or pebbles by wash of waves. Intermediate between the solution basins and the channels are potholes produced through me-

chanical abrasion by one or more cobbles that happen to become trapped in solution basins or other depressions in the beachrock.

Relationship to Beaches

In the Hawaiian Islands the maximum range of the tide is about 3 feet. Waves wash the beaches to a level ordinarily 2 or 3 feet higher than high tide. Little of the beachrock extends higher than the top of the wave-washed zone, but in several places it extends as much as 3 feet below low tide (west of Kahuku Point and at Hauula on Oahu; Nohili on Kauai; and Spreckelsville and Honokowai on Maui).

Most beachrock occurs on sandy beaches, usually with the same strike and dip as the layers of loose sand (Fig. 4). No beachrock was found at the ends of rocky points that project seaward between beaches, probably because of lack of sand.

In several places the beachrock, though at about the same height as the beach, has a different position in plan. The most conspicuous difference is shown by spits of beachrock that curve seaward away from the present beach, such as one at a point $1\frac{1}{2}$ miles west of Mokuleia on Oahu (Fig. 10), and near Honokowai and at five places between Kahului and lower Paia on Maui.

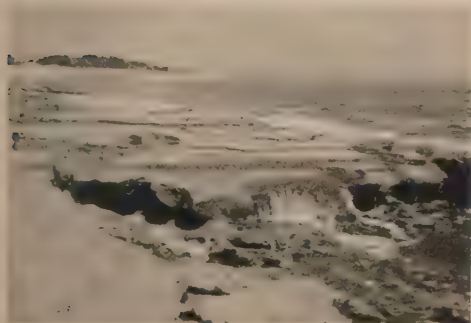


FIG. 9. Rimmed terraces in beachrock at Nohili, Kauai. Note narrow anastomosing ridges that separate the pools of different levels. These consist of beachrock, showing that the rimmed terraces are erosional rather than built up by deposition. Beachrock extends several feet, at least, below low water.



FIG. 10. Curved spit of beachrock near Mokuleia, Oahu, showing that considerable retreat of beach sand in background has occurred since the time of cementation of the beachrock.

More common are "whalebacks," or anticline-like masses of beachrock located immediately off the beaches. In these the strike parallels the beach, but the layers dip seaward and landward on opposite sides. Such whalebacks were observed at Paumalu, south of Laniloa Point, Keaau (Fig. 3), Makua, and 4 miles east of Kaena Point on Oahu. An intermediate feature, massive seaward-dipping beachrock that forms a sort of offshore bar, occurs at Waieli and Nohili (Fig. 11) on Kauai. In many of these and other localities, the beach has obviously undergone large recent losses of sand owing either to natural causes, or to mining by man, or to both. Retreat of some beaches is also shown by recent undercutting of trees, by exposure of very soft beachrock at the back of beaches, and by historical records.

Along the coast of Oahu from 1 to 3 miles east of Kaena and at Diamond Head, beachrock is present but present-day beaches are either absent or are very small. East of Kaena, at Waimea, and on both sides of the point 2 miles south of Makaha, small patches of beachrock lie atop reef rock that has been raised 5 to 7 feet above mid-tide. These patches have sufficient horizontal extent to differentiate them from sands that have accumulated in small pockets of reefs as shown in the raised algal reefs at Waimea on Oahu. South of Laniloa Point and elsewhere, massive

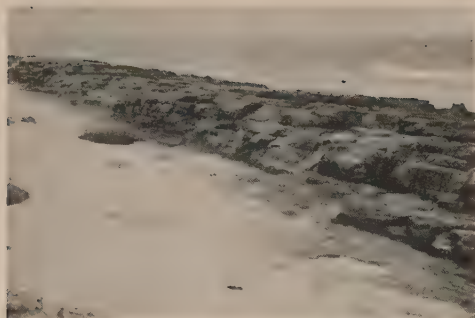


FIG. 11. Bar-like ridge of seaward-dipping beachrock just beyond beach of loose sand at Nohili, Kauai.

beachrock overlies reef rock and reaches as much as 10 feet above mid-tide. At Kaena Point a Pleistocene shoreline 95 feet above sea level (Stearns, 1935) is marked both by reef rock and by about 13 feet of beachrock. Raised reef rock capped by beachrock was observed on none of the other three islands.

In summary, the position and attitude of most beachrock is closely accordant with present beaches, but some beachrock is discordant with present beaches owing to retreat of beaches, or to coastal elevation or submergence after the beachrock was formed.

DISTRIBUTION AND HYDROLOGY

General

The shores of Oahu were examined more thoroughly than those of Kauai, Molokai, and Maui, because beachrock is more abundant and the shores are more easily accessible. After experience had shown the rarity of beachrock at the ends of rocky points, most

of the effort was spent on sandy bays between points. Altogether about 190 stations were made along the shores of Oahu, 100 on Kauai, 40 on Molokai, and 70 on Maui. Hawaii was not examined because beaches are rare and consist mostly of noncalcareous sand. Although Midway Island was not visited, Mr. J. A. Neff of the United States Fish and Wildlife Service (personal communication) reported the presence of slabby rock on Eastern Island that probably is beachrock. The results of the survey, based on measurements from the plottings on topographic maps, are presented in Table 3. Simplified plots for each of the four islands are given in Figures 12, 14, 16, and 17. Where no indication of beachrock or beach sand is given, the area was either not visited or was considered an impossible site for beachrock because of the absence of a sand beach.

It seems advantageous to describe very briefly the hydrology of the Hawaiian Islands because of the hypothesis that the development of beachrock is in some way controlled by the outflow of ground water through beaches. The hydrology of the four islands on which beachrock was studied is generalized in Figure 18.

The Hawaiian Islands consist of volcanic mountains built predominantly of basaltic lava flows and extending to heights of from 1,000 to 13,000 feet above sea level. Rainfall on these mountains is heavily influenced by the degree to which the moisture-laden winds, particularly the northeast trades, are forced upwards in their passage over or around them.

TABLE 2
COMPOSITION OF THIN-SECTIONS OF BEACHROCK SHOWN IN FIGURE 4

	PERCENTAGE OF AREA OF THIN-SECTION			PERCENTAGE OF ORIGINAL PORE AREA NOW FILLED
	Grains	Pore filling	Empty pores	
Loose slab.....	66	26	8	76
Layer G.....	57	33	10	77
Layer C.....	59	23	18	56
Layer B.....	56	15	29	35
Layer A.....	63	11	26	31

TABLE 3
GEOGRAPHICAL DISTRIBUTION OF BEACHROCK IN HAWAII

COAST	TOTAL MILES OF COAST	MILES OF SANDY BEACH EXAMINED	MILES OF BEACHROCK	PERCENTAGE BEACHROCK OF SANDY BEACH EXAMINED	PERCENTAGE BEACHROCK OF TOTAL COAST
Oahu					
Mokuleia to Paumalu.....	13.6	4.0	0.1	2	
Paumalu to Makahoa Pt.....	10.4	6.0	4.9	82	
Makahoa Pt. to Mokapu Pen...	33.6	20.8	1.0	5	
Mokapu Peninsula.....	11.2	1.7	1.5	88	
Kapoho Pt. to Waikiki Beach...	31.4	16.5	1.3	8	
Waikiki Beach to Pearl Harbor...	19.5	0.0	0.0?	0	
Pearl Harbor to Mokuleia.....	42.5	24.0	12.0	50	
Total.....	162.2	72.0	20.8	29	13
Kauai					
3 miles NE Nohili to Kealia....	47.4	10.2	2.6	25	
Kealia to Waimea.....	46.5	12.4	2.6	21	
Waimea to 3 miles NE Nohili...	16.6	13.0	2.6	20	
Total.....	110.5	35.6	7.8	22	7
Molokai					
4 miles E Hale o Lono to Kepuhi	15.2	7.5	4.8	64	
Kepuhi to Cape Halawa.....	50.9	0.0	0.0?	0	
Cape Halawa to 4 miles E Hale o Lono.....	38.2	9.0	0.0	0	
Total.....	104.3	16.5	4.8	29	5
Maui					
Maliko Bay to Makena.....	84.2	0.0	0.0?	0	
Makena to Lahaina.....	31.5	10.5	0.0	0	
Lahaina to Kahului.....	34.0	7.3	1.6	22	
Kahului to Maliko Bay.....	11.1	6.6	1.7	26	
Total.....	160.9	24.4	3.3	14	2
Grand Total.....	537.9	148.5	36.7	25	7

In areas of maximum rainfall, located on the windward slopes of the higher mountains and at the crests of the lower mountains, the mean annual rainfall is commonly in excess of 200 inches per year. On the leeward slopes the rainfall is generally much less than on the windward slopes, and on the lower parts of leeward slopes the mean annual rainfall may be less than 20 inches per year. The wide geographic variation in rainfall creates wide variations in both surface-water and ground-water resources.

There is surface runoff from all except the youngest terrains formed by fresh porous lava

flows. The courses of the streams are, however, so steep and short that the runoff alone creates flashy and, in the low rainfall areas, infrequent flows. However, many streams have cut valleys sufficiently deep to tap ground-water bodies that are perched on layers of comparatively low permeability interbedded in the generally highly pervious lava flows or are impounded between intrusive bodies in the central areas of the volcanoes, and have thereby developed perennial flows from springs. Much of the portion of the rainfall that infiltrates the surface does not reappear in high-level springs, but descends

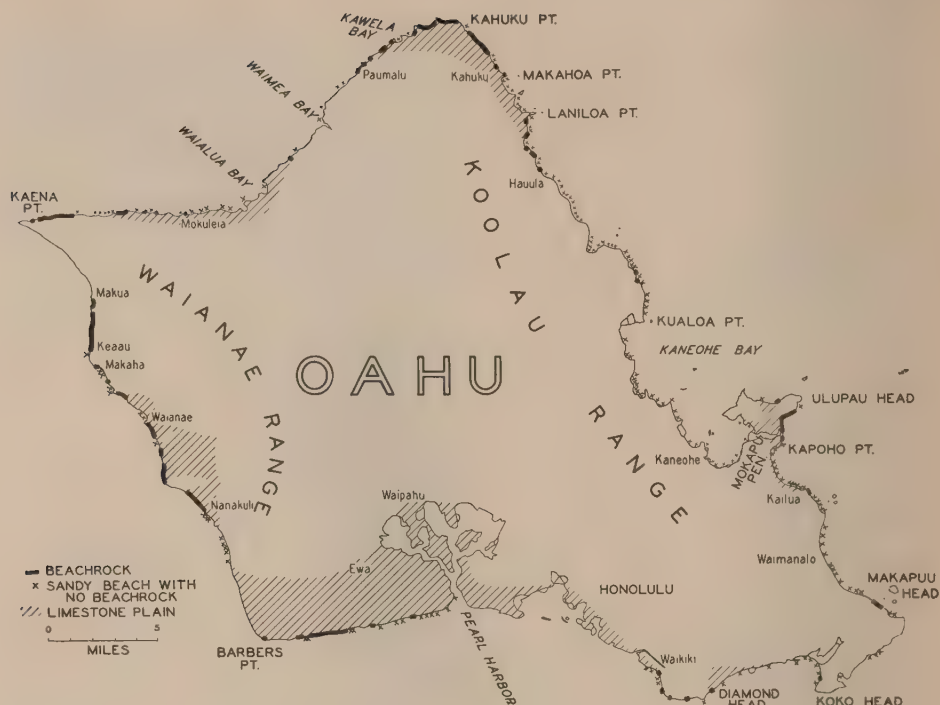


FIG. 12. Distribution of beachrock on Oahu.

to sea level in the lavas where it accumulates to form lenses of fresh water floating on the denser salt water penetrating from the sea. The thickness and freshness of these lenses depends in part on the amount of infiltration they receive and in part on the ease with which the water in them can drain seaward. Where the lavas crop out at the coast line there is generally easy outflow, and the lenses are thin. Particularly on the older islands, however, there may be extensive coastal plains underlain by prisms of sediments, partly coral and other limestones of generally high permeability, but also partly muddy sediments whose permeability is much lower than that of the lavas. Such sedimentary prisms constitute barriers restricting or diverting the ground-water outflow and causing the fresh-water lenses to be thicker in the bedrock behind such coastal plains.

Oahu

The northwestern coast of Oahu, from Mokuleia to Paumalu, is low, and two of the island's largest rivers enter at Waialua and Waimea Bays. Ground water stands comparatively high in the bedrock lavas behind the coast, except in a stretch a couple of miles each side of Waimea Bay, its height indicating that its drainage seaward is restricted by the sediments that make up the coastal plain. Springs create swamps on parts of the plain, and some of the drainage of these swamps may take place diffusely through the beaches, though the largest outflows are probably by way of the rivers and a few springs at or below sea level. Beachrock was found at only one locality (Fig. 12), not near a spring, where it dips seaward in the wave-washed zone.

The northern shore, backed by a wide limestone plain from Paumalu to Makahoa Point,

is characterized by an almost continuous strip of beachrock interrupted by a few sand-free projecting points. Within the bays, beachrock forms seaward-dipping strata as much as 4 feet thick atop reef rock (Fig. 4), though locally the beachrock is so thin that reef rock projects through it. The contact between reef rock and beachrock is commonly near the mid-tide level (Fig. 13). In most of this area the beachrock is in the wave-washed zone; but just east of Kahuku Point it rests on reef rock reaching to 5 feet above mid-tide, and just west of Kahuku Point it extends a foot or two below low tide. As it does farther west, the ground water stands high in the bedrock lavas back of this northern shore, and again leakage from the bedrock creates swamps and ponds in the limestone plain. The points of seaward drainage from these swamps are not known, but there are no conspicuous springs at or above sea level. No perennial streams reach the shore in this stretch of the coast.

Eastward from Makahoa Point the coastal plain narrows and is broken by stretches where bedrock lavas crop out at sea level. At such places there must be outflow of ground water, and at a few places there are visible springs at or just above sea level. The mountain rainfall increases eastward, the valleys are more deeply incised, and a number of perennial streams reach the shore between Makahoa Point and the base of Mokapu Peninsula.

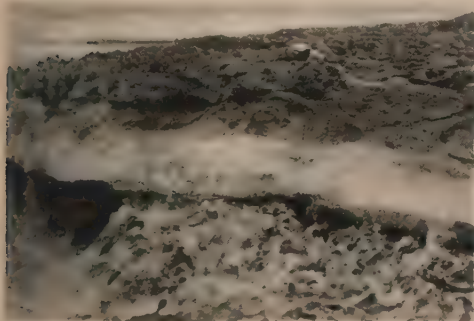


FIG. 13. Contact of beachrock atop reef rock near mid-tide level at a place one mile east of Kahuku Point, Oahu.

This shore contains little beachrock. Most of that which is present occurs between Laniloa Point and Hauula, where it forms thin seaward-dipping beds in the wave-washed zone except in the middle of the area where it rises from below mid-tide to 8 feet above mid-tide and is overlain by hard eolianite. About 1 mile south of Laniloa Point poorly cemented eolianite occurs at the base of a 10-foot cliff cut in dune sand. Beachrock was not found within Kaneohe Bay, an area of dilute sea water with many fish ponds along the shore. Islands within the bay are free of beachrock, perhaps because of the absence of loose sand, and, in the case of Coconut Island, because of artificial shores.

The Mokapu Peninsula consists of a core of late, relatively impervious, volcanic rocks and a surrounding limestone plain. The rainfall is low and there are no streams and probably very little ground water. Along shores on the eastern side of the peninsula there are extensive and massive beds of beachrock dipping seaward. Most of the beds are in the wave-washed zone, but near Ulupau Head some of the beachrock atop reef rock reaches to 10 feet above mid-tide. At Kapoho Point the reef rock is overlain by eolianite that has been truncated and drilled by potholes that later became filled by alluvium.

Over the eastern end of Oahu the rainfall decreases again, and no perennial streams drain to the coast east of Waimanalo and Honolulu. The permeability of even the bedrock is low in Kailua and Waimanalo on the windward side of the island, and although ground water stands relatively high in places, the amount of flow is probably not great. In the Honolulu area there are well-developed ground-water bodies in the bedrock whose seaward drainage is so restricted by coastal-plain sediments that most of the outflow probably takes place laterally to the coast through a limestone plain east of Diamond Head, and to Pearl Harbor, at the head of which there are very large springs. Makapuu Head is a mass of bedrock lavas cut into

cliffs at sea level. The rainfall is so low there, however, that there is probably very little ground water. Koko Head and Diamond Head are pyroclastic cones of low permeability and probably contain negligible ground water.

The shore of the southeastern part of Oahu from Kapoho Point to Waikiki Beach is mostly free of beachrock, although sandy beaches are abundant. Beachrock occurs in small thin patches near Kailua, northwest of Makapuu Head, near Koko Head, and around Diamond Head. At Diamond Head it lies atop a tuff terrace and beneath talus and eolianite in areas now free of loose beach sand. In all the areas except the one northwest of Makapuu Head, the beachrock is in the wave-washed zone; at this one place, a 1-foot layer of beachrock atop reef rock reaches to 8 feet above mid-tide.

Between Waikiki and Barbers Point, leakage from well-developed ground-water bodies in the bedrock lavas and seepage from streams have created thin fresh-water lenses in, and swampy spots on, the surface of the coastal plain, much of which is composed of limestone. No notable shoreline springs are known, however, except the Pearl Harbor springs previously mentioned, which represent drainage direct from the bedrock. From Barbers Point northwest to Makaha the bedrock ground-water bodies are less well developed because the rainfall is much lower. There are still thin lenses of ground water in the coastal-plain sediments as far as Makaha, at least, but again no notable shoreline springs are known. No perennial streams reach the shore. The Kaena Point area at the western end of the island is very dry.

Shores between Waikiki Beach and the entrance of Pearl Harbor are so altered by man that they were not investigated. Beginning at the entrance of Pearl Harbor and extending around Barbers Point and Kaena Point to Mokuleia, the coast is dominated by beachrock except at projecting sand-free points. Between the entrance of Pearl Harbor and

Barbers Point beachrock alternates with loose sand, with a general westerly increase in abundance of beachrock. Where present, the beachrock is restricted to the wave-washed zone. The 4-mile stretch of coast northwest of Barbers Point and the 5-mile section southeast of Kaena Point were not visited because of the lack of roads. Lava reaches the shore most of the way in the latter stretch (Wentworth, 1938: 8). Along most of the rest of the Waianae shore, beachrock is almost continuous except on the projecting points. The beachrock is almost equally divided between massive beds in the wave-washed zone (Fig. 2) and thin patches atop reef rock to heights of 5 to 8 feet above mid-tide. At Keaau it is interbedded with alluvium (Fig. 3). About half of the shore of abundant beachrock is backed by a wide limestone plain (Fig. 12), but in the northern part, from Keaau to Makua, only the beach separates the lavas from the sea.

Kauai

The island of Kauai has had a more complex structural history than the other Hawaiian Islands. As a consequence, the permeability of its rocks is in general lower and the amount of ground water smaller in relation to surface water.

The western half of the northern coast, from 3 miles northeast of Nohili nearly to Haena Point, consists of cliffs cut into bedrock lavas and is inaccessible except by foot or boat. Sand beaches are rare and no beachrock has been found.

Most of the rest of the northern coast, the eastern coast, and the southern coast to Waiimea, consist of gentle slopes or low cliffs cut in relatively late lavas of generally low permeability. Numerous perennial streams reach the sea, and beaches at their mouths are common. In addition, there is a narrow coastal plain extending with minor breaks for about 5 miles south from Kapaa. Southwest of Nawiliwili Bay for 5 miles the coast consists of cliffs similar to those of the northwestern



FIG. 14. Distribution of beachrock on Kauai.

coast. Beachrock is present in many small patches along these coasts, none more than 0.3 mile long (Fig. 14) and all consisting of thin seaward-dipping beds in the wave-washed zone. About a half dozen occurrences between Haena and Kealia are at the mouths of small to moderately large streams, in contrast with the absence of beachrock in such places on Oahu.

The western coast, between Waimea and a point 3 miles northeast of Nohili, is backed by a limestone plain that reaches a width of 2 miles. The surface of the plain was once largely covered by a swamp fed by intermittent streams and by leakage of ground water from the bedrock lavas in cliffs back of the plain, but the swamp has been artificially drained.

Along the seaward margin is a wide high sandy beach locally backed by dunes. A local fisherman reported that the northernmost part of the beach has become considerably wider in the past few years and in this area no beachrock is exposed. The escape of fresh ground water through the beach sand is notable 3 miles northeast of Nohili, where the coastal plain pinches so that the beach rests directly against the bedrock cliff. In the middle of the area, at Nohili, there is a 2-mile exposure of massive beachrock (Fig. 11) reaching about 4 feet above mid-tide and at least 3 feet and possibly 8 feet below mid-tide. The uncertainty is due to slumping of large blocks of the beachrock due to the erosion of some undetermined softer material

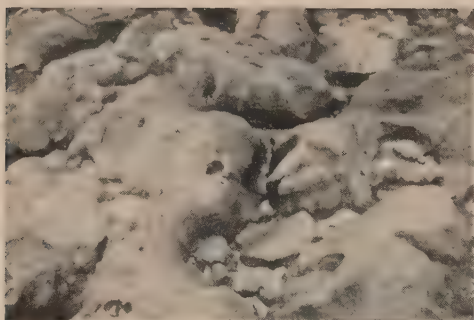


FIG. 15. Beachrock at Nohili, Kauai, showing solution basins having rounded and smoothed surfaces believed to indicate modification of ordinary sharp-edged solution basins 'during' a period of burial under loose beach sand followed by exhumation.

underlying it. The slumped blocks range up to 30 by 15 by 5 feet. A shorter exposure of beachrock at Waieli has been transected by a drainage ditch that reveals progressive decrease of cementation of the beachrock at depth. Some of this beachrock has a rounded and smoothed surface (Fig. 15), unlike beachrock elsewhere which is undergoing active solution. This is presumed to indicate a former exposure of the beachrock followed by burial under thick sand, and finally exhumation by recent retreat of the beach. Judging from the massive nature of beachrock at both Nohili and Waieli, it seems likely that this entire section of the western

coast is underlain by beachrock that now is exposed only where recent retreat of beach sand has occurred. Retreat of the beach has also exposed very poorly cemented beachrock and eolianite landward of the main mass of beachrock at Nohili.

Molokai

The eastern part of Molokai has a high rainfall, and is well drained by both surface streams and ground-water flow. Particularly along the southern coast a few miles south of Cape Halawa to a few miles west of Kaunakakai the escape of ground water at sea level is notable. The western part is very dry with no perennial streams and only brackish ground water.

Beachrock on Molokai is confined to the southwestern and western coasts, from a point 2 miles east of Hale o Lono to Kepuhi (Fig. 16). A 4-mile continuous exposure of beachrock, the longest seen in the islands, centers at Hale o Lono. Within the wave-washed zone and seaward-dipping, most of this beachrock is slabby and some of it has been quarried for building purposes. In the area north of Laau Point beachrock is slabby like that at Hale o Lono, but it reaches to 8 feet above mid-tide. The bay near Kepuhi contains some of the most massive beachrock seen in the islands, reaching from below mid-tide to 10 feet above it. The surface is highly polished



FIG. 16. Distribution of beachrock on Molokai.



FIG. 17. Distribution of beachrock on Maui.

and locally is discolored by blue-green algae. Elongate erosional channels are well developed.

From Kepuhi around Ilio Point to Cape Halawa, the coast is precipitous with only two sandy beaches. At one of these places, Kalaupapa, possible but uncertain beachrock was noted from a vantage point at the top of the high cliff about 2 miles away. This is believed to be the only possible site of beachrock along the entire northern coast of Molokai. The southern coast from Cape Halawa to Hale o Lono was examined closely without finding any trace of beachrock. Scattered along almost the entire shore are artificial fish ponds in which mullet and other brackish-water fish are cultivated. Muddy sediments have accumulated along the more protected parts of this shore. *Ulva*, or sea lettuce, is very abundant along the shores, forming local drifts about a foot thick.

Maui

Less beachrock was found on Maui than on any of the other islands examined, a total of 3.3 miles of shoreline length (Fig. 17). The absence of sand beaches around most of East Maui, from Maliko Bay to a point 2 miles south of Makena, means that the presence of beachrock is very unlikely, so the available field time was concentrated in more favorable areas.

No perennial streams reach the shores of East Maui from Kahului Bay to Maliko Bay except at Maliko, nor from Maalaea Bay to far east of Makena. However, east of the two bays, the bedrock lavas extend to the shores with only a thin discontinuous mantle of beaches, so that ground water escapes easily at or near sea level. On the southern coast the ground water is brackish and probably not plentiful, but there must be a substantial outflow along the northern coast. It is noteworthy that there is beachrock on the northern coast, but none on the plentiful beaches of the southern coast. The beachrock on the northern coast consists of an interesting series of five spits and bars, between Spreckelsville and Lower Paia, and occurrences in the wave-washed zone in two bays northeast of Lower Paia. In one of these bays and at the small point north of Spreckelsville beachrock overlies red soil, and at the latter site it also directly overlies a basaltic flow in places. More beachrock is shown in offshore positions in this area than elsewhere in the islands, and the remnants are also farther offshore, suggesting that retreat of sand beaches has been great. Recent retreat is also indicated by undercutting of trees and by historical records. Some of the sand may have been transported to the southwest and added to the beach near Kahului where no beachrock could be found, but additional sand has been removed for construction purposes. One of the beaches at Spreckelsville was covered with drifts of *Ulva*.

Narrow coastal plains, in which no beachrock was found, front Maalaea Bay and Ka-

hului Bay. Cliffs form the coasts of West Maui for 3 miles west of Maalaea Bay on the south, and from Kahului Bay around Naka-lele Point nearly to Honokowai on the north. The few sandy beaches on these shores do not contain beachrock.

The rest of the coast, on the west and southwest, consists of a narrow coastal plain. Judging from the low and fairly uniform height of the ground water in the bedrock back of the coastal plain, there must be fairly plentiful points of ground-water escape, but none are known at or above sea level. South of Lahaina there are no exposures of beachrock, but 2 miles to the north there is a small outcrop and another mile farther north there

are loose slabs of beachrock. Near Honokowai beachrock in the wave-washed zone extends along more than a mile of shore, in some sections forming a spit or bar 20 to 50 feet offshore of the present beach. Locally, two bars are present. Along some of this shore, recent retreat of a 10-foot cliff of alluvium is indicated by undercutting of large trees, and this retreat is in part responsible for exposing some beachrock. Except for two small outcrops just north of Mahinahina Point, a mile north of Honokowai, beachrock is absent around the rest of West Maui.

AGE

In most areas the beachrock could have been formed very recently, even within the

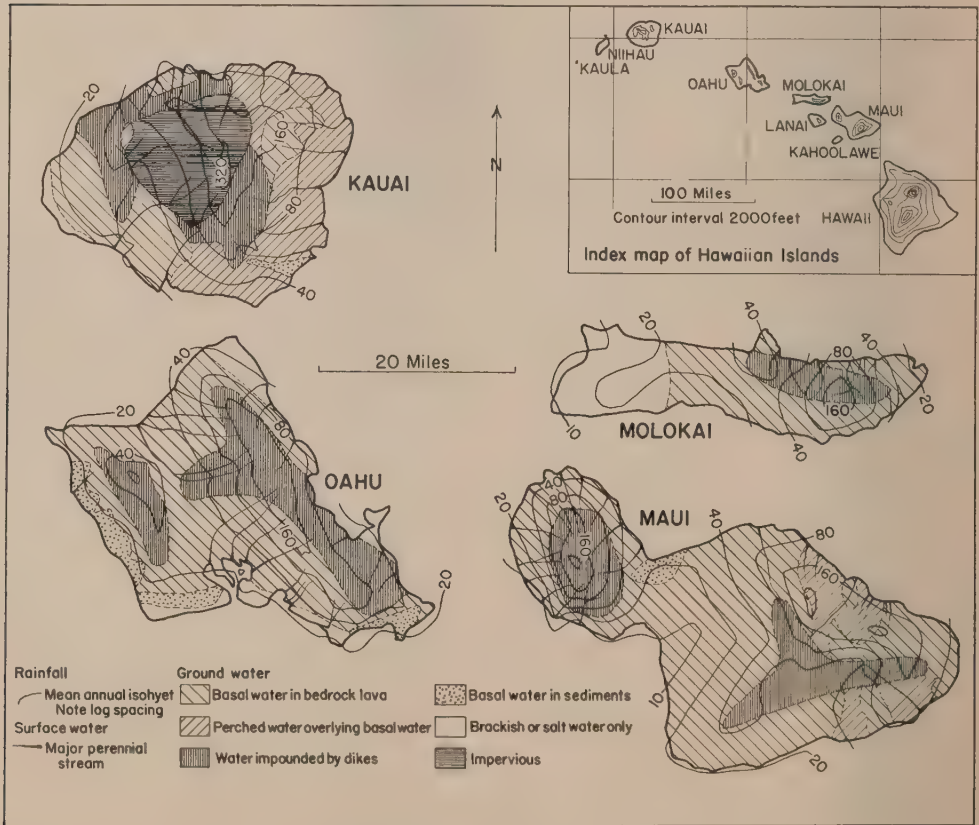


FIG. 18. Map showing hydrology of Kauai, Oahu, Molokai, and Maui.

last decade. A recent age is suggested by the common restriction of the beachrock to positions within the wave-washed zone and to the similarity of its strike and dip to those of the present beach. A somewhat greater age in other places may be indicated by differences in the positions of the beachrock and the present beach (i.e., presence of beachrock spits and whalebacks) indicating retreat of the beach since the beachrock was formed. A locally greater age is also indicated by interbedding of beachrock with other materials. Alluvium is interbedded or overlies beachrock at Waianae and Keaau on Oahu. Near Lower Paia on Maui beachrock rests on red soil that is now intertidal in position.

Some beachrock must be older, and of a greater age than nearby intertidal beachrock, for on Oahu it occurs on raised reef rock as much as 10 feet above present sea level. Elsewhere, $\frac{1}{2}$ and $2\frac{1}{2}$ miles south of Laniloa Point and at Diamond Head on Oahu, beachrock is overlain by eolianite, which at Diamond Head is itself overlain by talus. The greatest age of all, Pleistocene, is indicated for beachrock on the 95-foot Kaena terrace of Oahu.

In summary, beachrock in the Hawaiian Islands may be of three different ages: modern to a few thousand years old (wave-washed zone); probably several to many thousand years old (on raised reef rock and/or overlain by alluvium or eolianite); and Pleistocene age (Kaena terrace). In addition, it is evident that even the youngest of these three ages represents not a single stage of cementation, but rather several to many separate stages. Repeated stages of cementation are well shown by the common presence of reworked beachrock slabs incorporated in later layers and by truncation of earlier layers by later ones.

ECONOMIC VALUE

Beachrock of many tropical islands has long been used for minor construction purposes, such as grave markers and flagstones. Some has also been used to make "flint" artifacts.

Slabs of beachrock were quarried from near Hale o Lono on Molokai and transported to Honolulu for decorative use in buildings. It has also been quarried near Barbers Point on Oahu, according to Stearns (1939). Many other beaches are capable of supplying such slabs. From still other localities solid dimension stone, 2 to 4 feet in smallest dimension, can be obtained. Among the best of these localities are: bays on both sides of Kahuku Point, two areas just south of Laniloa Point, and two areas just south of Waianae on Oahu; at Waieli and Nohili on Kauai; and at Kepuhi on Molokai. The economic value, however, is not great because the cut stone probably would have an appearance very similar to concrete made from loose beach sand.

Beachrock has also been found to constitute the best source, on atolls, of aggregate for concrete. The rock is quarried, crushed, screened, and mixed with cement and sea water to form a good grade of concrete (Narver, 1954).

ORIGIN

The main purpose of this investigation was to discover, if possible, the origin of beachrock—at least of the beachrock in the Hawaiian Islands. Altogether, beachrock was noted along approximately 37 miles of the shores, but in such a variety of environments that it is difficult to isolate the least common denominator, or most probable controlling factor.

Absence of beachrock at the ends of points and other areas where loose beach sand is not now present, nor probably ever was present, leads to the obvious conclusion that loose beach sand must be available if beachrock is to form. Beyond this point, generalizations appear to have many exceptions.

Before making the present study, the authors recognized that beachrock is abundant around islets of atolls and relatively rare around high islands of moderately great rainfall such as Guam. The hypothesis was developed that beachrock occurs where the in-

terstitial water of beaches is sea water, which is already saturated with calcium carbonate, and that it should be absent where the interstices are occupied by ground water that has passed only through volcanic rocks and is presumably not saturated with calcium carbonate. In addition, beachrock should be present where the beach contains ground water that has escaped from a wide limestone plain and thus contains a high percentage of calcium carbonate. The basis for this hypothesis is that water that is left in the beach by a falling tide or that rises by capillarity through the beach sand largely evaporates near the sand surface. Any salts originally dissolved in the water are precipitated in the sand where they serve as a cement (Emery and Foster, 1948). Readily soluble salts such as sodium chloride are removed by the next high tide, but salts such as calcium carbonate may remain to form a more permanent cement. In addition, the heating of the beach by the sun during the day tends to reduce the solubility of CO_2 in the interstitial water close to the surface, so that its pH rises. If the water is initially near saturation, calcium carbonate is precipitated (Emery, Tracey, and Ladd, 1954: 45-46). Because sea water contains more calcium carbonate than most ground waters, it seems reasonable to expect that beach sands would be cemented into beachrock more easily where sea water is evaporated than where only fresh water containing little calcium carbonate is evaporated.

On Oahu the hypothesis appears to be supported generally by field data. Beachrock is

abundant along the western coast where the rainfall is low and on Mokapu Peninsula, also a low rainfall locality. Conductimetric tests show that interstitial beach water in these areas is sea water; therefore, it is probable that little ground water escapes through these beaches. One of the chief areas of beachrock on Oahu is the northern coast around Kahuku Point, an area where considerable quantities of fresh water escape and where conductimetric and titration tests showed that ground water is associated with beachrock. Titration of four water samples from the bottom of the deepest hole of Figure 5, of three from the loose beach sand, and of three from the ocean water atop the reef flat, yielded average chlorinity values of 2.50, 3.58, and 19.14 parts per thousand, respectively. Comparison of the calcium and chloride concentrations (Table 4) shows that both ions are less abundant in water collected from the hole in beachrock than in sea water, but that the calcium concentration with respect to chloride is about twice as great as in sea water. This high ratio of calcium to chloride in the ground water means that much of the calcium must have been derived from the rocks through which the water passed. Some additional support for the hypothesis can be obtained by consideration of the areas where beachrock is absent. Very little beachrock occurs along most of the eastern coast of Oahu where high rainfall leads to escape of large amounts of surface and ground water. No beachrock whatever is known in Kaneohe Bay, where sea water was found to be diluted

TABLE 4
COMPOSITION OF WATERS

	CALCIUM ppm	CHLORIDE ppm	Ca/Cl	SOURCE OF DATA
Hole through beachrock of Figure 5..	144	2,610	0.0552	USC analysis by Dr. Wilson Orr
Sea water (general).....	400	18,980	0.02106	Sverdrup, Johnson, and Fleming (1942: 173)
Sea water (Hanauma Bay).....	507	19,681*	0.0258	Stearns and Vaksvik (1935: 361)

* Includes nitrate.

by fresh water escaping from volcanic rocks or flowing atop an alluvial plain.

On Molokai the distribution of beachrock fits the hypothesis even better. Beachrock is well developed along the western and south-western shores, where escape of ground water is probably small because the rainfall is low. Beachrock is absent along the rest of the southern shore. This coast, though itself low in rainfall, receives much ground water from the main ridge of East Molokai which has a high rainfall. Because of the considerable escape of ground water, the nearshore sea water has been diluted, especially in the large artificial fish ponds that were built in ancient times. Brackish water in these ponds supports a crop of mullet, a fish that prefers fresh or brackish water (Hiatt, 1944). In the same area *Ulva*, sea lettuce, is prolific (Abbott, 1947), suggesting that it too prefers dilute sea water. The only other areas of abundant fish ponds are along Kaneohe Bay and the southeastern shore of Oahu, and here also beachrock is absent.

On Maui a reversed situation exists. Beachrock is absent or rare around the leeward coast of low rainfall and probably little ground water, but abundant near Lower Paia where considerable dilution by ground water is known. In this area the ground water comes directly from the volcanic rocks to the beach, as it does along the southern shore of Molokai. Thus, on Maui the distribution of beachrock does not fit the original hypothesis.

On Kauai, as on Maui, beachrock appears to be independent of the kind of interstitial water. The most extensive area of beachrock is the western alluvial coast, a situation similar to the dry western coast of Oahu where beachrock is abundant. However, beachrock also occurs in small patches around other shores of Kauai, and some of these patches lie at the mouths of perennial streams.

Altogether, the evidence from distribution shows no unequivocal preference of beachrock for beaches having interstitial water composed of sea water, ground water from lime-

stone plains, or ground water from volcanic rocks. If the nature of the interstitial water were a dominant control, we must be prepared to say either that areas which now contribute much ground water directly from volcanic rocks formerly contributed little ground water, and that beachrock in those areas was formed during the past, or that details in the pattern of the ground-water flow, not predictable except possibly by a study more intensive than that reported, lead to important variations in the nature of the interstitial water in the beaches. The first conclusion does not appear to be reasonable, and the second begs the question. We must look, therefore, for other possible explanations or for supplementary factors.

One such explanation was proposed by Cloud (1952) who suggested that blue-green algae, known to live in the top quarter-inch of some beach sands, may cement the sand through their biochemical activities. Cementation of individual layers, 2 feet or more thick, appears to be a fatal objection, because the algae are probably restricted to the top-most fraction of an inch in order to receive enough sunlight for photosynthetic activities. Another possible explanation proposed by Nesteroff (1955: 33) and Ranson (1955) is that amorphous calcium carbonate is deposited between the sand grains by the action of bacteria living in organic material deposited with the sand. However, there seems to be no evidence of the presence of large amounts of organic material in the Hawaiian beachrock and the organic content of the sand is extremely low (Oahu samples 1, 5, 8, 15, and 16 of Table 1 have organic carbon percentages of only 0.10, 0.16, 0.14, 0.22, and 0.09, respectively).

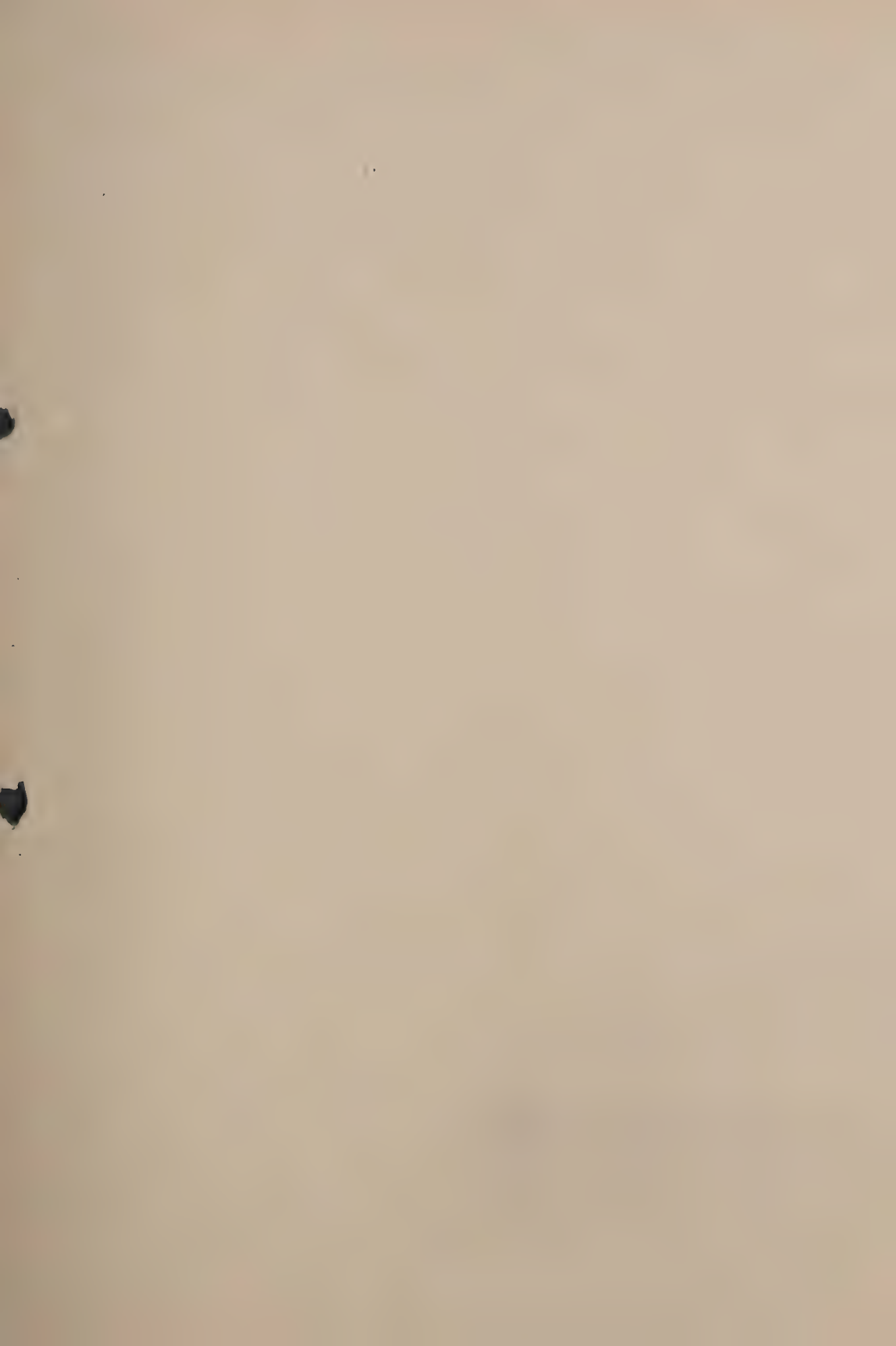
Merrin (1955), who studied beachrock in Puerto Rico, proposed that beachrock is restricted to areas of stable beaches; however, many of the Hawaiian beaches having beachrock are known to undergo large changes seasonally and because of storms. In fact, some of the areas of beachrock on Kauai

shown by Figure 14 were covered by sand at the time of our mapping and were discovered by Dr. Douglas Inman of Scripps Institution of Oceanography during a later visit.

In short, although beachrock is abundant in the Hawaiian Islands and elsewhere, we do not know how it forms. Mapping its distribution is not by itself a sufficient source of data to solve the problem of origin. Perhaps the making of many additional chemical analyses of interstitial waters of beaches would be a helpful supplement to mapping.

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The Probable Method of Fertilization in Terrestrial Hermit Crabs Based on a Comparative Study of Spermatophores¹

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ALTHOUGH the physiological and mechanical phenomena of the vasa deferentia resulting in the elaboration of the spermatophores of marine hermit crabs (Pagurida) have been investigated (Mouchet, 1931; Matthews, 1953), these phenomena in terrestrial hermit crabs (*Coenobita* and *Birgus*) have been neglected. Spermatophores of marine hermits are made with precision; the so-called immutable form of their acuminate capsules is often distinctive of the species. These capsules, "elevated" on slender stalks, are admirably adapted for aquatic dissemination of the spermatozoa. Because marine hermit crabs are regarded as the progenitors of terrestrial hermit crabs, the present study was undertaken to reveal whether the form of the aquatic spermatophore has become modified in the change to a terrestrial environment, and if so, to consider, in lieu of actual observation, whether these modifications are of sufficient magnitude to make tenable the common assumption that in terrestrial hermits fertilization occurs on land.

METHODS AND TECHNIQUES

The method employed was to study the phenomena of spermatophore elaboration in (1) a truly aquatic hermit crab, (2) a "transi-

tional" terrestrial hermit with gastropod shell, and (3) a terrestrial hermit, no longer protected by a gastropod shell. For the typical aquatic hermit, *Dardanus punctulatus* (vide Edmondson, 1946: 265) was selected. These were taken at Oahu, Territory of Hawaii, between June, 1953, and July, 1954. *Coenobita rugosus*, the selected "transitional" hermit, and *Birgus latro*, the selected terrestrial hermit, were taken at Eniwetok Atoll (Marshall Islands) between September 1, 1954, and September 15, 1954.

The abundant *C. rugosus* were easily collected but the scarce *B. latro* had to be dug from their burrows. These hermits were killed and dissected at the Marine Laboratory at Eniwetok. There, the male reproductive systems, for purposes of routine histological examination, were placed in Bouin's fixative, cleared in toluene, embedded in Tissuemat (54°-56° C.), sectioned at 10 microns, stained with standard alum-haematoxylin and counterstained with eosin (0.5 per cent solution in 90 per cent alcohol to which 0.4 cc. of 0.1 N HCl was added). Some testis sections of both aquatic and terrestrial hermits were stained with Heidenhain's iron-haematoxylin without a counterstain, while others were stained with safranin (Grubler's "Safranin O") and counterstained with light green. Because the large, proximal portions of the vasa deferentia of both aquatic and terrestrial hermits became extremely brittle after fixation, and were sectioned only with difficulty, sim-

¹ Contribution No. 77, Hawaii Marine Laboratory. Manuscript received September 7, 1955.

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ilar unfixed portions were immersed for 10–30 minutes in an aqueous solution of toluidin blue (1–10,000), teased open in sea water, and their vitally stained contents studied.

OBSERVATIONS

Macroscopic Observation of Abdomens

When removed from the protective gastropod shell, the soft, vulnerable abdomen of *D. punctulatus* is seen to be twisted in accordance with the clockwise helical shell. Although five tergal plates are clearly discernable, they are weakly sclerotized. Pleopods are present only on the left side. The uropods are highly modified and serve primarily as hold-fasts.

Removal of the protective gastropod shell from *C. rugosus* discloses an abdomen which approximates that of *D. punctulatus*. Again the soft abdomen is twisted in compliance with the spiral shell and although five tergal plates are present they are poorly sclerotized. As in aquatic hermits, the pleopods are present only on the left side. Again the uropods are modified for attachment.

The unprotected abdomen of *B. latro* (*vide* Harms, 1932: figs. 1, 2, 3, 4) is straight, stubby, and its broad tergal plates are more heavily sclerotized than either those of *D. punctulatus* or *C. rugosus*. Pleopods are again restricted to the left side. The uropods are modified and reduced but obviously serve no longer as hold-fasts.

Macroscopic Observations of Dissected Abdomens

Typical of the dissected abdomens of aquatic hermits is (Matthews, *op. cit.*, fig. 2-b, p. 257) that of *D. punctulatus* in which a large, paired, hepatopancreas almost fills the entire abdominal cavity. The hepatopancreas, because of connecting mesenteries, carries the testes and vasa deferentia as it follows the turns of the abdomen and is largely responsible for the asymmetrical visceral arrangement. As in other aquatic hermits which inhabit

right-handed shells, the right testis and right vas deferens are crowded and somewhat reduced.

The dissected abdomen of *C. rugosus* is almost identical with that of *D. punctulatus*. Again the large hepatopancreas almost fills the abdomen and carries with it the crowded testes and vasa deferentia and again this results in the reduction of the right testis and right vas deferens.

The dissected abdomen of *B. latro* reveals a large hepatopancreas joined to the other viscera by mesenteries. The testes and vasa deferentia are neatly fitted between the right and left portions of the hepatopancreas. Slight differences in size of testis and vas deferens are observed, but the smaller occurs on the right or left side indiscriminately.

The living vasa deferentia of *D. punctulatus*, *C. rugosus*, and *B. latro* exhibit spasmodic, muscular contractions (*vide* Matthews, 1953: 258). However, the opacity of the vasa deferentia prevents the actual observation of the effects of these contractions on the pliable sperm mass. But, as will be shown subsequently, these contractions serve both to move the sperm mass along and to mold it in compliance with gradual changes in the conformation of the vasa deferentia.

Microscopic Examination of Sectioned Testes

The sectioned testis of *D. punctulatus* is a highly coiled, continuous, thin-walled tube into which numerous sacculi open (*vide* Matthews, 1953: 258, fig. 3). The sacculi in cross section are observed in all stages of maturity. The immature sacculus is filled with large primary spermatocytes; others, more mature, are filled with spermatids in all stages of metamorphosis. These are expelled from the sacculus into a minute collecting tubule of the testis by the proliferation of new primary spermatocytes from the germinal epithelium of each sacculus. In other words, the old metamorphosing spermatids are crowded or pushed out of the sacculus by the development of new primary spermatocytes. The

study of many sacculi reveals this to be a rhythmical process. This process produces a continuous sperm mass. This undifferentiated sperm mass enters the small, proximal vas deferens (*vide* Matthews, 1953: 259, fig. 6).

Fundamentally, the sectioned testis of *C. rugosus* resembles that of *D. punctulatus*. The sacculi open into a minute, highly coiled collecting tubule. Sacculi are seen in all stages of maturity. Except for slight differences of detail, the process of filling the sacculi with primary spermatocytes and the expulsion of metamorphosing spermatids is identical with that of *D. punctulatus*. Again the combined, rhythmical, saccular activity provides a continuous, undifferentiated sperm mass which enters the proximal portion of the vas deferens.

The sectioned testis of *B. latro* resembles those of *D. punctulatus* and *C. rugosus*. Sacculi in all stages of maturity are observed and again their rhythmical activity fills the minute collecting tubule with metamorphosing spermatids. The differences observed are primarily of size, the sacculi of *D. punctulatus* and *C. rugosus* being generally smaller than those of *B. latro*. Also observed were slight differences in the number and arrangement of sustentacular cells (*vide* Matthews, 1954: 116, fig. 2b). Although these were present in all sacculi whose spermatids were metamorphosing, their fate still remains obscure.

Microscopic Examination of Sectioned Vasa Deferentia

Cross sections through the proximal portion of the vas deferens of *D. punctulatus* reveal a minute cylindrical tube with a thin wall of contractile tissue and cuboidal epithelium, the almost circular lumen of which is completely occupied by a discoidal portion of the continuous, rod-shaped sperm mass (*vide* Matthews, 1953: 259, fig. 6). Except for slight differences in size, comparable portions of the proximal vasa deferentia of *C. rugosus* and *B. latro* appear identical with those of *D. punctulatus*.

In *D. punctulatus*, as the vas deferens gradually increases in diameter the once circular lumen becomes ellipsoidal (*vide* Matthews, 1953: 260, fig. 7). This change in shape of the lumen is the result of the bounding epithelial cells which have become columnar except at the more pointed extremities of the lumen where cuboidal epithelium still persists. An acidophylic secretion from these cuboidal cells lines the lumen but later surrounds and adheres to the sperm mass to form the thin, sperm mass sheath (*vide* Matthews, 1953: 261, fig. 9). In compliance with the change in shape of the lumen, the sheathed sperm mass becomes ellipsoidal. In *C. rugosus* and *B. latro* cross sections through comparable regions of the vas deferens also reveal ellipsoidal lumina and sheathed sperm masses.

In *D. punctulatus*, cross sections of the vas deferens reveal that the ellipsoidal lumen gradually becomes pear-shaped and that the sheathed sperm mass becomes folded into arches (*vide* Matthews, 1953: 262, fig. 10). A new secretion arises from the epithelial cells at the more pointed end of the lumen; this secretion fills the spaces between the closing arches and forms the "upright" stalks (*vide* Matthews, 1953: 262–263, figs. 11, 12, 13). As this secretion accumulates, the stalks lengthen and the ampullae of sperm are carried "aloft."

In *C. rugosus* and *B. latro* a similar change from an ellipsoidal to a pear-shaped lumen is observed and, accompanying this change, the contained, sheathed, sperm mass is folded into arches. In like manner a secretion, arising from epithelial cells of the pointed end of the lumen, fills the spaces between the closing arches and forms the "upright" stalks. Again, as this secretion accumulates, the stalks lengthen and "elevate" the closing arches to form the ampullae of sperm.

In *D. punctulatus*, *C. rugosus*, and *B. latro* (Fig. 1a–c) still another secretion is given off by the epithelial cells (*ep.*) bordering the lumen which surrounds the "upright" stalks (*st.*) and ampullae (*am.*) and forms the veil

(v.). In *D. punctulatus* the groove of the lumen is deep and results in the formation of tall, thin spermatophores (Fig. 1a). In *C. rugosus* (Fig. 1b) and *B. latro* (Fig. 1c), the groove is shallow and results in the formation of short, broad spermatophores.

DISCUSSION

The spermatophores of *D. punctulatus*, *C. rugosus*, and *B. latro* are formed with great precision. The spermatophores of any one *D. punctulatus* are similar to those of any other of its species. In like manner, the spermatophores of *C. rugosus* and *B. latro* do not vary within the species. However, only in this restricted sense is it permissible to refer to the spermatophores of any one species as being immutable. Because immutable precludes change, its use in connection with spermatophores is untenable. What is probably meant by the use of this term is that, for any one species at the time of observation, spermatophores appear identical. Surely, the complicated mechanical and physiological phenomena associated with spermatophoric development have evolved throughout the ages and these changes have been accompanied by changes in spermatophores.

Although in *D. punctulatus* the actual process of copulation has not been observed, there is little doubt that it occurs in water. This species does not frequent the shallow reef waters and, so far as is known, never comes ashore even at night. Specimens taken in fishermen's nets frequently show spermatophores attached to both body and gastropod shell. This same attachment of spermatophores is also observed in this species at the Honolulu Aquarium where, prior to spermatophoric deposition, males are frequently seen dragging females about. However, since copulation probably takes place at night, it has not been possible to observe the process in these captive specimens. Moreover, as these specimens are afforded no opportunity to leave the tanks, copulation and the subsequent process

of fertilization must occur in water. Therefore, the possibility of terrestrial copulation and fertilization in free living specimens remains but seems rather unlikely.

The spermatophores of *C. rugosus* (Fig. 2b) resemble closely the spermatophores of *D. punctulatus* (Fig. 2a). There are obvious differences in size of ampullae, upright stalks, veil, etc., but the fundamental plan is the same. This fact, coupled with similarities of spermatophoric development, strongly suggests that for this species the rate and extent of adaptive changes in the reproductive system did not parallel the rate and extent of other terrestrial adaptations. The similarity of these spermatophores with those of *D. punctulatus* should not be interpreted as due to the immutability of *C. rugosus* spermatophores, but rather, that at the particular time of observation, the spermatophores of *C. rugosus* had not "progressed" beyond the aquatic spermatophore level attained by *D. punctulatus*.

Again, copulation and the subsequent process of fertilization in *C. rugosus* have not, to the author's knowledge, been recorded. Even though *C. rugosus* in certain of its organ systems is admirably adapted for a terrestrial habitat, caution should be exercised in assuming that all organ systems are equally so adapted. The literature is replete with reference to the female's dependence on the sea. Harms (1932: 260 [translated]) states:

The East Indian "Coenobites" seem to spawn all year long, but they seem to reach a climax in the months of January to March. During those months I observed how flocks of *Coenobita cavipes* and [*C.*] *clupeatus* wandered during the night toward the coast of Perbaengan (East coast of Sumatra) in order to deposit their zoëa into the water. At the end of May till the beginning of July I observed how the beach swarmed with "Coenobites" in all phases of metamorphosis. . . . On the the island of Siberoet I saw the same thing between May 31 to June 5, 1929, but here *Coenobita rugosus* were involved. The young "Coenobites" emerge from the water with tiny snail-shells, and live at first amphibiously.

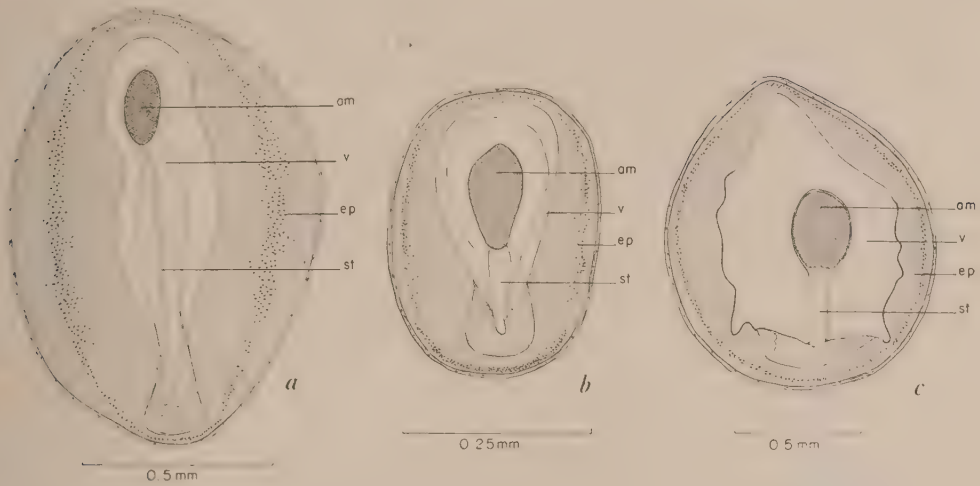


FIG. 1. Diagrammatic cross section of the vas deferens of: *a*, *Dardanus punctulatus*; *b*, *Coenobita rugosus*; *c*, *Birgus latro* showing: *am.*, ampulla; *v.*, veil; *ep.*, veil-producing epithelium; *st.*, stalk.

Again in reference to "Coenobites" dependence on the sea, Dr. Yoshio Kondo, terrestrial malacologist of the Bernice P. Bishop Museum, informs me (*in litt.*) that on Saipan swarms of these land crabs make monthly, full-moon migrations to the sea. At this time they are gathered by the bushels for food and, so far as is known, both males and females are taken. The possibility therefore exists that these nocturnal migrations may serve purposes other than the moistening of the gills or the deposition of zoëa.

At Eniwetok I observed both male and female *C. rugosus* on the beach at night although I did not observe any in the water or in the act of copulation. Because females are observed with spermatophores both on their bodies and on their gastropod shells, and because the tubelike extensions on the coxopodite of the fifth pereiopods are too large to serve as penes, it appears quite unlikely that an internal deposition of spermatophores takes place. Both the origin and the aquatic form of *C. rugosus* spermatophores suggest that copulation and fertilization occur in water.

The spermatophores of *B. latro* (Fig. 2c)

resemble closely the spermatophores of *D. punctulatus* (Fig. 2a) and *C. rugosus* (Fig. 2b). There are obvious differences in size of ampullae, upright stalks, veils, etc., but again, the fundamental plan is the paguridan aquatic spermatophore. As in *C. rugosus*, this fact, coupled with the similarity of their spermatophoric development, strongly suggests that in *B. latro* also the rate and extent of reproductive adaptations did not parallel the rate and extent of other adaptations. Again, this is not an example of the immutability of spermatophores but rather, at the time of observation, the spermatophores of *B. latro* had not "progressed" beyond the level of the aquatic spermatophore attained by *D. punctulatus*.

Harms (*op. cit.*: 262 [translated]) in reporting on the reproductive activity in *B. latro* says:

The process of copulation is at this time still unknown. The males do not have special organs for copulation. Yet copulation must take place, and seems to do so on land, since females are found at great distance from the coast. The sperms are probably transmitted by means of spermatophores. In response to excitation I got the male to emit masses of sperm [spermatophores]. These hardened subsequently. . . .

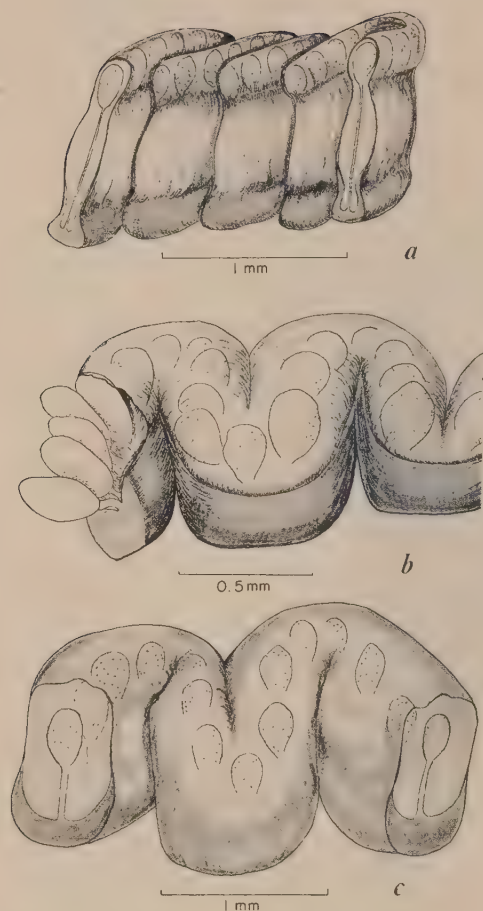


FIG. 2. Portion of vitally stained spermatophore of: a, *Dardanus punctulatus*; b, *Coenobita rugosus*; c, *Birgus latro*.

The possibility exists that these gummed up masses of sperm are transferred to the female . . . the development inside the egg goes as far as the zoëa, which has been described by Borradaile [1900]. . . . *Birgus* has a typical paguride zoëa, which resembles on the whole the zoëas of *Spiropagurus* and of *Eupagurus*. . . . The peculiarity of the zoëas of *Birgus* lies in a certain simplification of its over-all organization, illustrated especially by the absence of otherwise typical bristles and teeth. Perhaps it can be assumed with certain confidence that further development up to the metamorphosis takes place exactly as with the rest of the pagurids, especially the "Coenobites."

Harms (1937: 14) further states that the eggs are fertilized at the place of deposit and become attached immediately. He does not say however, how or where this process takes place.

According to the observations of Andrews (1900) on Christmas Island, *B. latro*, too, like the "Coenobites" wanders in great flocks to the sea in the months of January to March. Presumably both males and females take part in these migrations and the possibility exists that in this case, as with *C. rugosus*, the purpose might be for copulation as well as the deposition of zoëa.

At Bikini in July 1947 Dr. Robert Hiatt observed numerous zoëa in the water in which a berried female had been contained overnight. He also observed berried females with their abdomens immersed in intertidal pools liberating zoëa.

Because this part of the reproductive cycle of *B. latro* requires an aquatic environment it appears likely that the liberation of sperm from the spermatophore and fertilization are aquatic. This would not obviate the possibility of a terrestrial attachment of the spermatophore. However, the similarity in the development of spermatophores in the "terrestrial" *C. rugosus* and *B. latro* and in the truly aquatic *D. punctulatus*, seems to argue for the assumption that copulation and the subsequent process of fertilization are also aquatic in these terrestrial species. Surely, this assumption is more valid than the assumption that for these species fertilization takes place on land, "since females are found at great distance from the coast." Without attempting to explain what has brought about modifications for a terrestrial existence, modifications of the reproductive system are not as urgent as, for example, those of the respiratory system which must be used continuously once emergence has occurred. Reproduction, although obviously important to maintain the species, is not a continuous process, therefore, not of primary urgency for the survival of the individual. When necessary, the crabs can return

to their old habitat, water, as do the Amphibians.

In lieu of actual observation to the contrary the modifications of the spermatophores of *C. rugosus* and *B. latro* are not of sufficient magnitude to make tenable the common assumption that terrestrial hermit crabs are fertilized on land. Stationed at a likely spot, a patient observer, equipped with an infra-red light, may provide the ultimate solution to this problem by direct observation of copulation and fertilization in terrestrial hermit crabs.

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Contributions to the Knowledge of the Alpheid Shrimp
of the Pacific Ocean

Part I. Collections from the Mariana Archipelago¹

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Reprinted from PACIFIC SCIENCE
July, 1956

Contributions to the Knowledge of the Alpheid Shrimp of the Pacific Ocean

Part I. Collections from the Mariana Archipelago¹

ALBERT H. BANNER²

THIS IS THE FIRST of a planned series of papers on the distribution in the Pacific of the shrimp of the family Alpheidae (previously Crangonidae; name of the family and of the type genus, *Crangon*, changed by action of the International Commission for Zoological Nomenclature in February 1955, Opinion 334). A large series of collections has been made available to me. The collections were taken over a broad sweep of the Pacific, from the Tuamotus in the east to the Marianas in the west and I have supplemented these by personal collections. The series of publications will consider the collections archipelago by archipelago, and I hope to conclude them by a summarizing paper giving all citations to published works dealing with the Indo-Pacific species and full records of distribution for each species.

This work has been undertaken in the hope that these shrimp, the most common on the reefs, the most easily collected and preserved, may prove to be of value as zoogeographical and ecological "indicator organisms." Such indicator species could be used as they are used in plankton analyses to characterize and recognize certain ecological groupings correlated with the physical environment. At this

early stage it is not known whether these species will prove of value in this respect.

Inasmuch as the concluding paper will carry all bibliographic citations to previous work in the Pacific, the individual papers will carry references only to the original descriptions of the species and to other papers used in the identification of the species.

The measurements used and the names of the ridges and grooves of the large chela in the genus *Alpheus* are the same as in my paper on the snapping shrimp of Hawaii (1953: 4, 59).

COLLECTIONS AVAILABLE

There are two major collections available from Saipan. The first I made while I was stationed there in the United States Army Air Force during the years 1944 and 1945. Unfortunately, world wars do not lend themselves well to biological collecting, and I was fortunate to be able to obtain as many specimens as I did. Perhaps half of the specimens I collected, together with all of my field notes on the localities and environments of the collections, were lost. As a consequence, I cannot assign the species to more than the general locality of Saipan. Most of my collections were made on the beach and narrow fringing reef called Unai Obyan; a few were made in various parts of the broad lagoon west of the island; none were made in Bahai

¹ Contribution No. 79, Hawaii Marine Laboratory. Manuscript received September 12, 1955.

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Laulau or on the north and east sides of the island because those areas were largely "out-of-bounds" with guerrilla action still taking place. The only station which I can positively identify is that for the collection dated 25 December 1944. It was made on the eastern side of the fringing reef before our camp, close to Cape Naftan; the water was about 3 feet deep within the "lagoon" of the fringing reef, the bottom was largely sand and extending above the water level were large boulders, upon the lower parts of which living coral was growing. This is the type locality for two new subspecies.

The other collection was made by Dr. Preston E. Cloud, Jr. and his party during the course of a geological survey of Saipan and is in the United States National Museum. Fortunately, there are thorough notes on the habitats of these specimens. The localities of the stations are shown in Figure 1; information on the habitats is given below:

A-5—1 mile offshore, depth 28 feet. Limesand bottom surrounds areas of what appear to be bare coral-algal limestone in horizontal layers. Scattered over the surface of the rock patches and also on the limesand are irregular blocks of dead coral. Patches of bright orange sponge were observed, but neither living plants nor corals were noted. April 6, 1949.

A-7—1.2 miles offshore (immediately south of uncovering reef SE of Mañagaha islet); depth 24 feet. Even to very slightly undulating bottom of fine- to coarse-grained limesand. April 6, 1949.

C-1—About 1,200 feet offshore; depth 10 feet. Limesand plain, dominantly coarse-grained and well sorted, with minor reef prominences up to about 20 feet in diameter. April 9, 1949.

C-7a—About 1.4 miles offshore; depth 8–9 feet around coral-algal bosses that rise to or near surface along line of transverse. Between coral and coral-algal masses the bottom is thinly coated with limesand, through which one can scrape to a hard undersurface of



FIG. 1. Saipan, Mariana Archipelago, $13^{\circ} 20' N$, $140^{\circ} 40' E$, showing collecting stations. The geographical designations are given in the local, non-anglicized, names (courtesy of Dr. P. E. Cloud, Jr.). Outer dotted line represents 100 fathoms, inner dashed line 10 fathoms. (Adapted from U. S. Hydrographic Office Chart 6060.)

crustose coralline algae with bare hands. April 10, 1949.

D-5—About 0.6 mile off Muchot point between reef clusters at south side of Saipan harbor; depth 5–15 feet. Generally similar to D-6 (see below), but with rocky bottom and a lesser total area of limesand nearby. Bottom at immediate point of collecting is one of mostly dead coral-algal rock with a fairly rich veneer of living crustose coralline algae. It rises to within five feet of the water surface at some places, but has deep cracks, channels, pothole-like depressions, and irregular depressions, some floored with angular gravel of broken coral and algal material. Into and cutting across this irregular rock surface are

limesand-floored channels up to perhaps 10 feet deep (15 feet below water surface) and for the most part sharply undercut into the base of the bordering overhanging coral-algal rock. May 6, 1949.

D-6—About 0.8 mile off Muchot point, near entrance to Saipan Harbor; depth 4–17 feet. Point of anchorage at a depth of 4 feet over the edge of a very irregular reef surface in which the primary builders of the present time are crustose coralline algae. Green algae are fairly abundantly scattered over the irregular reef surface, and into it extend tongues of clean limesand with ripple marks aligned approximately parallel to the reef front. These limesand tongues merge seaward with larger areas of limesand at depths of 15–17 feet. In pothole-like depressions on the reef surface are minor accumulations of angular gravel of broken coral and coralline algae. May 6, 1949.

D-7—About 1 mile off Muchot point, near entrance to Saipan Harbor; depth 22 feet. Collecting point immediately south of a mooring buoy over a narrow tongue of limesand between two rocky mounds—the one to the east rising about 12 feet above the bottom and being perhaps 100 yards long. Although drab and dead-looking, the surfaces of these and similar nearby mounds have a large proportion of living, purplish pink, crustose coralline algae. This calcareous algal growth, however, appears to be mostly a surface veneer over dead coral centers, a scattered growth of living coral still persisting in spots that have not been completely covered over by algae. May 6 and 13, 1949.

D-8—About 1.3 miles off Muchot point, immediately east of outer channel buoy, entrance to Saipan harbor; depth 36–42 feet. Bottom dominantly of dead coral-algal rock with irregular patches and thin local veneers of limesand and coral-algal rubble. Living coral and crustose coralline algae are found only as occasional bits on the generally dead and rocky surface, perhaps because of the general murkiness of the water here at the

harbor exit. The individual rocky mounds are low, rising to an approximately consistent level only a few feet above the intervening limesand. May 13, June 26, 1949.

E-4—About 0.4 mile offshore; depth 5–9 feet. Bottom of calcareous gravel and coarse limesand, interspersed with patches of ramose coralline algae. May 3, 1949.

E-7—About 0.9 mile offshore just beyond seaward edge of south limb of barrier reef west of Saipan; depth 25–34 feet. Bottom is a rough and irregular rocky surface of dead coral and coral-algal material on which are occasional patches of veneering limesand. A few small patches of veneering coral were seen, and a little living coralline algae; but most of the floor is dead rock with a scattering of encrusting green algae. May 3, 1949.

E-8—About 1.1 miles offshore, just north of Schildkrote Rock, seaward from the barrier reef west of Saipan; depth 32–38 feet. Bottom is very rocky, rising abruptly to Schildkrote Rock, which has points within two feet of mean low tide. May 4, 1949.

FX—About 0.7 mile offshore, depth less than 6 feet at low tide. Calcareous gravel and limesand bottom at inboard edge of reef. April 18, 1949.

LOC. 2—North side of passage into Saipan harbor. Depths 40–45 feet over bottom of interspersed limesand and patch reefs. Specimens taken from a half-ton coral rock brought up on a ship's anchor and broken up with sledge hammers and picks. April 28, 1949.

LOC. 6—Just north of Mañagaha islet in lagoon west of Saipan. Collections from lagoon fringe of barrier reef. June 1949.

LOC. 8—In shoal water over broad fringing reef at northwest end of barrier-fringing reef complex west of Saipan. Depths less than 6 feet at low tide. Knolls of dead coral-algal rock and living corals common on calcareous gravel and limesand bottom. Various times between December 1948 and June 1949.

LOC. 9—Fanunchuluyan Bay at northeast end of Saipan. Sand and gravel platform covered by as much as 5 or 6 feet of water at low

tide and locally with numerous irregular bosses of coral-algal rock and patchy coral growth behind seaward edge of a fringing reef, 300 to 700 feet wide. December 25, 1948.

Further information on these stations and the marine ecology of Saipan may be found in Cloud's chapter, "Marine Geology and Shoal Water Ecology" in the forthcoming *Geology of Saipan*.

In addition to these two collections, there is one specimen reported in this study that was collected on Guam (about 100 miles south of Saipan) by a Mr. Seale in 1900 which is in the Bernice P. Bishop Museum of Honolulu.

Cloud's study on Saipan was made under the sponsorship of the United States Geological Survey and the Corps of Engineers, United States Army. The present study was begun with support from a grant administered by the United States National Museum and the Pacific Science Board under a contract between the Office of Naval Research, Biology Branch, and the National Academy of Sciences (NR160-175); some help in the final typing was obtained with funds from a National Science Foundation grant (NSF-G-1754).

The specimens collected by Cloud, together with the type specimens from my collection, will be deposited in the United States National Museum; the disposition of my personal collection has not yet been decided and it may be deposited either in the National Museum or in the Bernice P. Bishop Museum.

AUTOMATE de Man

Automate *johnsoni* Chace

Automate johnsoni Chace, U. S. Natl. Mus., Proc. 105 (3349): 13, fig. 7, 1955.

LOCALITIES: Banner, 2 specimens in 2 collections; Cloud 1 specimen each at D-8, E-7, E-8.

DISCUSSION: Of the five specimens in the collection, only one, an ovigerous female, had the chelae intact.

It is difficult to decide how these few fragmentary specimens should be named. *A. johnsoni* is at least very closely related to *A. gardineri* Coutiére (1905: 854), and, in the opinion of Chace, perhaps identical with it. In the series of slight differences between the two forms, the specimens from Saipan are somewhat intermediate, and appear to differ from both forms in yet other ways.

The rostrum in *A. gardineri* is rounded and separated laterally from the margins of the carapace by slight grooves, whereas in *A. johnsoni* and in the present specimens it is anteriorly rounded and without lateral grooves. The eyes in *A. gardineri* are variable in shape, but are irregular on the lateral and anterior margins according to the figures, whereas in *A. johnsoni* and the Saipan specimens the peduncles and corneas present a smooth curve from the base to the anterior medial margin. Chace points out that the second antennular article is 2.5 instead of 4.0 times as long as broad in his specimen; however, according to Coutiére's figures the proportions in his type and cotype vary from 3 to 4 times as long as broad, and he states in his text that the proportions vary with the size of the specimen; in the Saipan specimens the proportion is about 3 to 1. In both *A. gardineri* and these specimens the stylocerite does not reach to the end of the first article, and the scaphocerite does not reach past the middle of the second article of the antennules, whereas in *A. johnsoni* the stylocerite exceeds the first article in length and the scaphocerite reaches within 0.2 of the end of the second article. Further, the superior surface of the ischium of the large chela bears a strong spine in the Saipan specimens, a weak spine in *A. johnsoni*, and lacks a spine (according to the figures) in *A. gardineri*; neither Coutiére nor Chace show or discuss any rounded teeth on the dactylus of the large chela, yet they are quite easily seen on the chela of these Saipan specimens. Finally, in the second legs the first two articles are shown to have a ratio of 10:18 by Coutiére, 10:12 by Chace, and are about 10:13

in the Saipan specimens (the right and left carpi have slightly different proportions in the distal articles of the intact female).

I suspect that the differences between *A. gardineri*, *A. johnsoni*, and the Saipan specimens are either individual variations or geographic differences of only subspecific worth, but until more complete specimens are examined from other areas, it would be best to leave the two species standing. These specimens from Saipan have been placed in *A. johnsoni* because of the similarity of the anterior carapace and rostrum.

ATHANAS Leach

Athanas djiboutensis Coutière

Athanas djiboutensis Coutière, Paris Mus. d'Hist. Nat., Bul. 3(6): 234, 1897a; Soc. Philomath. Paris, Bul. IX, 5(2): 75, 1903, and Fauna and Geogr. Mald. and Laccad. 2(4): 856, 1905. [These two identical papers are partial redescriptions.]

Athanas sulcatipes Borradaile, Zool. Soc. London, Proc., [1898]: 1011, pl. 65, fig. 9, 1898.

LOCALITIES: Banner, 22 specimens in 6 collections. Cloud, 3 at locality A-5, 1 at A-7, 3 at C-7a (13 May 1949), 2 at D-5, 2 at Loc. 8, 1 at Loc. 6.

DISCUSSION: These specimens agree well with the original and the redescription of Coutière, except for several points of variation both of which have been remarked upon before by Tattersall (1921: 367-368). The first is the length of the rostrum in respect to the antennular peduncle, described by Coutière (1905) as reaching "presque l'extrémité du pédoncule antennulaire"; in this large series of specimens only few approach this length, while most reach to near the end of the second antennular article and a few reach only the middle of the same article. A second point of variation is found in the form and armature of the large chela of the males. On this appendage the ischium bears from one (as shown by Coutière) to four strong mov-

able spines; the outer inferior margin of the merus may be entire, bear a slight rounded indentation, or be divided into two shallow and broad lobes, the distal approximately half the length of the proximal; the palm of the chela proper varies, being both slightly thicker and less tapering than is shown by Coutière, and, in proportion to the fingers, the palm is relatively longer; finally, the dactylus may be strongly curved and cross the immovable fingers as shown by Coutière, or be less curved and meet the opposite exactly. The conical protuberance of the carpus of the small chela of the female may be lacking and the surface of the carpus away from the chela may be rounded. No great significance is attached to these variations, especially as they have been previously noted by Tattersall, and as the variations appear independently of each other in the individual specimens.

The eyes appear to have some degree of motion, they may be either extended from under the carapace or withdrawn slightly. This small motion would not be noteworthy except that in this species and in other members of this genus the lengths of the circum-orbital spines are often compared relative to these corneas as part of the specific description.

Athanas dubius sp. nov.

Fig. 2

TYPES: Holotype a 7.3 mm. ovigerous female, collected from Saipan by A. H. Banner; allotype a male 7.8 mm. long and 7 paratypes collected by A. H. Banner in three collections; 1 paratype collected by P. E. Cloud, Jr., from locality E-8. Types to be deposited in the U. S. National Museum.

DESCRIPTION: Rostrum acute, triangular, sides not curved, tip reaching to end of second antennular article (Fig. 2a has somewhat foreshortened rostrum); rostrum and carapace rounded, without carina. Supracorneal spines not reaching to middle of cornea; carapace between base of supracorneal spines and ros-

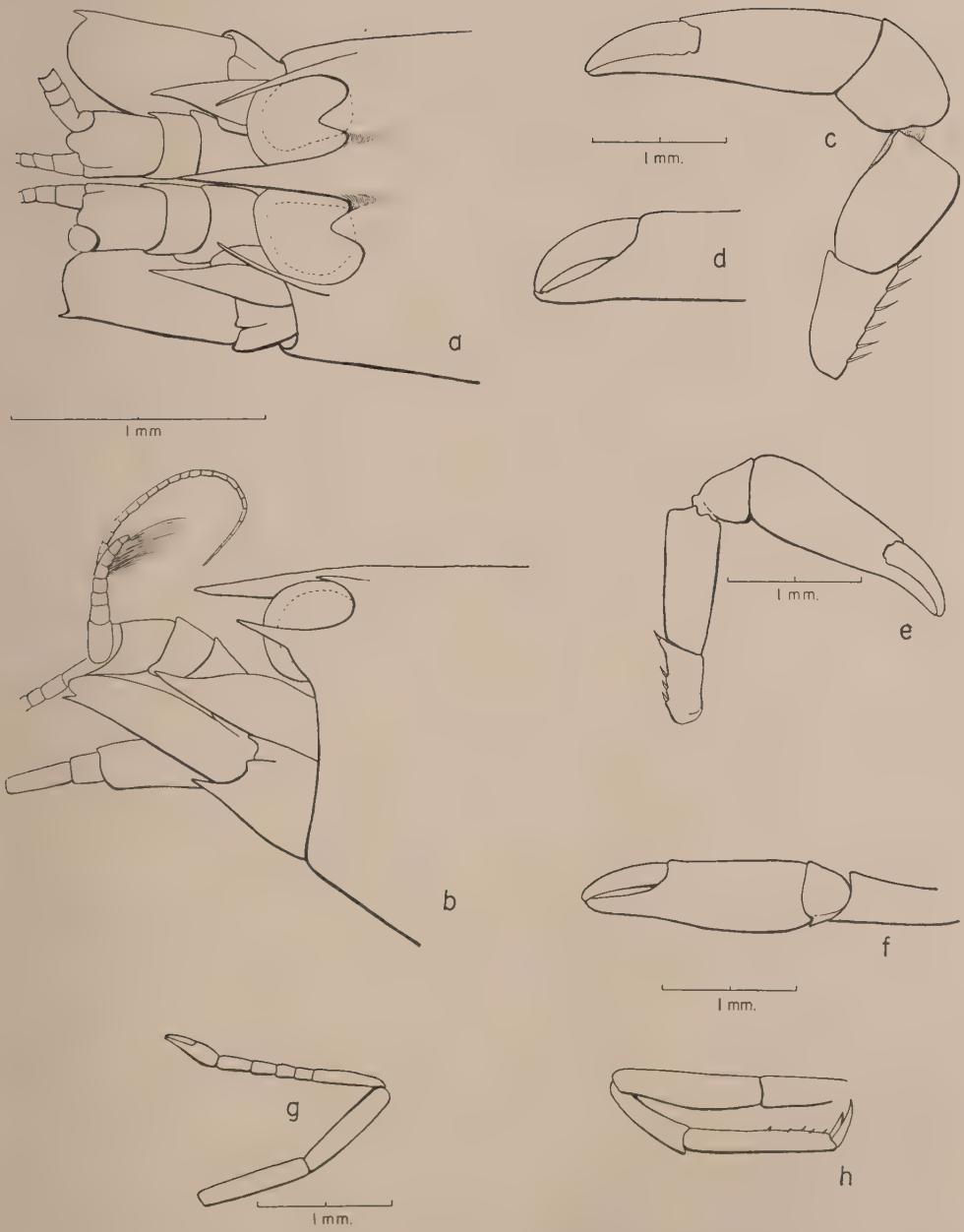


FIG. 2. *Athanas dubius* sp. nov. a, b, Anterior region, dorsal and lateral aspects; c, cheliped, male; d, large chela, finger, male; e, cheliped, female; f, chela, propodus and merus, female; g, second leg; h, third leg.

trum slightly depressed. Extracorneal spines strong, acute, reaching beyond corneas almost to end of first antennular article. Infracorneal spine absent, represented by a slight convexity on inferior margin of extracorneal spine. Pterygostomial angle rounded.

Portion of first antennular article in front of corneas about equal in length to second antennular article, latter about half as long as third article. Stylocerite acute, reaching end of second article. Lateral spine of basicerite reaching end of first antennular article. Scaphocerite with lateral spine very slightly longer than rounded portion, reaching slightly beyond end of antennular peduncle. Carpo-cerite shorter than scaphocerite.

Chelipeds showing slight sexual dimorphism and, in some cases, asymmetry. In type (female), large chela about 7 per cent longer than small chela, both of similar form. Ischium bearing four strong spines; merus unarmed, about 2.5 times as long as broad; carpus rounded, somewhat elongate, with distal end enclosing base of palm; chela almost cylindrical, slightly inflated proximally, three times as long as broad, with fingers occupying about distal third; fingers without teeth, dactylus slightly curved. Large chela in allotype slightly over 10 per cent longer than small chela, but of similar form. Ischium 0.8 as long as merus and bearing six strong spines; merus heavy, 0.6 as broad as long, half as long as chela, unarmed; carpus heavy, cylindrical and fitting over base of chela; chela cylindrical, tapering, 0.3 as broad as long, with fingers occupying slightly less than distal third; fingers unarmed, dactylus curved distally.

Carpal articles with ratio: 10: 2.6: 3.2: 3.7: 5.9.

Ischium of third legs unarmed, 0.5 as long as merus; merus unarmed, 0.2 as broad as long; carpus 0.6 as long as merus, 3 times as long as broad; propodus equal in length to merus, bearing 5 small spinules in distal half, terminal movable spine 0.6 length of dactylus; dactylus 0.3 length of propodus,

simple, slightly curved and gradually tapering to acute tip.

Telson half as wide posteriorly as anteriorly, 3.6 times as long as posterior margin is broad; sides straight with uniform taper; distal margin moderately convex; both dorsal spinules located posterior to middle.

Eggs of type specimen 0.32×0.50 mm. in diameter.

DISCUSSION: In the group of paratypic specimens some variations are found, especially in the armature of the chelipeds. The number of spines on the ischium in the females varies from three to six, usually five or six; in the males the spines, always stronger than those of the female, vary in number from five to six. In some of the males the distal external angle of the merus is produced into a strong but rounded lobe; in one female the superior angle of the distal end of the merus carries a rather weak movable spine. Further, the degree of asymmetry varies from chelae that are equal to to slightly more asymmetrical than those of the types. Finally, on one female the carpus of the second legs on one side is divided into four articles while the other has the normal five. No marked variation was noticed in the other parts of the body or appendages.

The validity of this species is somewhat questionable for it is closely associated with *A. areteformis* Coutière (1903: 79; 1905: 860) and *A. erythraeus* Ramadam (1936: 13). Unfortunately the description of neither of these two species is complete. All three belong to the *nitescens* group of the genus in which the chelae are carried directed forward. All three also have simple dactyli on the posterior legs, the supracorneal spine well developed, the extracorneal spine greatly produced, and the infracorneal spine wanting. *A. dubius* differs from *A. areteformis* in that the dactylus of the large chela of the male is relatively longer, being over 0.6 the length of the palm in the former and 0.3 the length of the palm in the latter; in the latter, moreover, this dactylus is strongly curved. In comparing the chelae

of the female of *A. dubius* to *A. naifarøensis* (which Coutière states "... ne diffère aucunement. . .") it is found that the palm is less expanded in *A. naifarøensis*, being without taper and having its breadth equal to only half the length of the fingers, instead of being equal to the length of the fingers as in *A. dubius*, also the ischium is unarmed in *A. naifarøensis* whereas in *A. dubius* it bears 3-6 spines.

There are also slight differences between *A. dubius* and *A. erythraeus*. Ramadam states that in the latter the sides of the rostrum are parallel for some distance from the proximal end, whereas in the former there is a uniform taper from the base to the tip; in his specimen, a female, the fingers of the chela have slightly rounded teeth, two on the side of the dactyl, one on the immovable finger, and in mine the fingers bear straight knife-like cutting edges.

However, these differences, and the differences between *A. erythraeus* and *A. areteformis*, are very slight, and the similarities, especially in the form of the anterior carapace and appendages, are great. It is reasonable to expect that when specimens are collected at localities between Ghardaqa in the Red Sea and the Maldivé and Laccadive archipelagoes in the Indian Ocean and between these archipelagoes and the Marianas, intermediate forms may be found.

ARETE Stimpson

Arete iphianassa de Man

Arete iphianassa de Man, Ned. Dierk. Ver., Tidschr. II, 11(4): 312, 1910; Siboga Exped., 39a¹(2): 164, pls. 3-4, fig. 11, 1911.

LOCALITIES: Cloud, 4 specimens at locality C-7a (2 each on 10 April and 13 May, 1949), 1 at D-8, 1 at Loc. 6.

DISCUSSION: These six specimens agree almost exactly with de Man's description and figures except that the tooth on the dactylus of the large chela of the male is less pronounced than shown in de Man's figure 11a.

ALPHEOPSIS Coutière

Alpheopsis equalis Coutière

Alpheopsis equalis Coutière, Paris Mus. d'Hist. Nat., Bul. 2(8): 380, 1896.

Alpheopsis aequalis de Man, Siboga Exped., 39a¹(2): 177, 1911.

LOCALITIES: Banner, 17 specimens in 5 collections; Cloud, 1 specimen at Loc. 6.

DISCUSSION: These specimens show much of the variation in the rostrum, pterygostomial angle, coverage of the eyes, and in the large chelae like that already reported from Hawaii (Banner, 1953: 16). In addition they present several variations worthy of note. First, the base of the rostrum in most specimens is set off from the anterior portion of the carapace by definite angles, but in one specimen the margins of the carapace are continuous in a gradual concave curve to the tip of the rostrum, and in several specimens the condition is intermediate. Second, the ratio of the middle articles of the carpus is also variable, with the second article running from a third shorter to a third longer than the third article; the ratio of the lengths of the third and fourth articles also varies but less conspicuously. Finally, in a specimen normal in all other respects the carpus of the second leg is divided into six, rather than five articles. This development is symmetric, and the extra article appears to be equal in length to the normal third article and is adjacent (either proximal or distal) to it.

Alpheopsis diabilus, sp. nov.

Fig. 3

TYPE: A 9.2 mm. ovigerous female, collected by A. H. Banner.

DESCRIPTION: Anterior portion of carapace produced as short, triangular rostrum reaching two-thirds of length of visible portion of first antennular article, and as triangular extracorneal spines about half the length of rostrum; without ridges or depressions. Pigmented portion of cornea concealed in dorsal

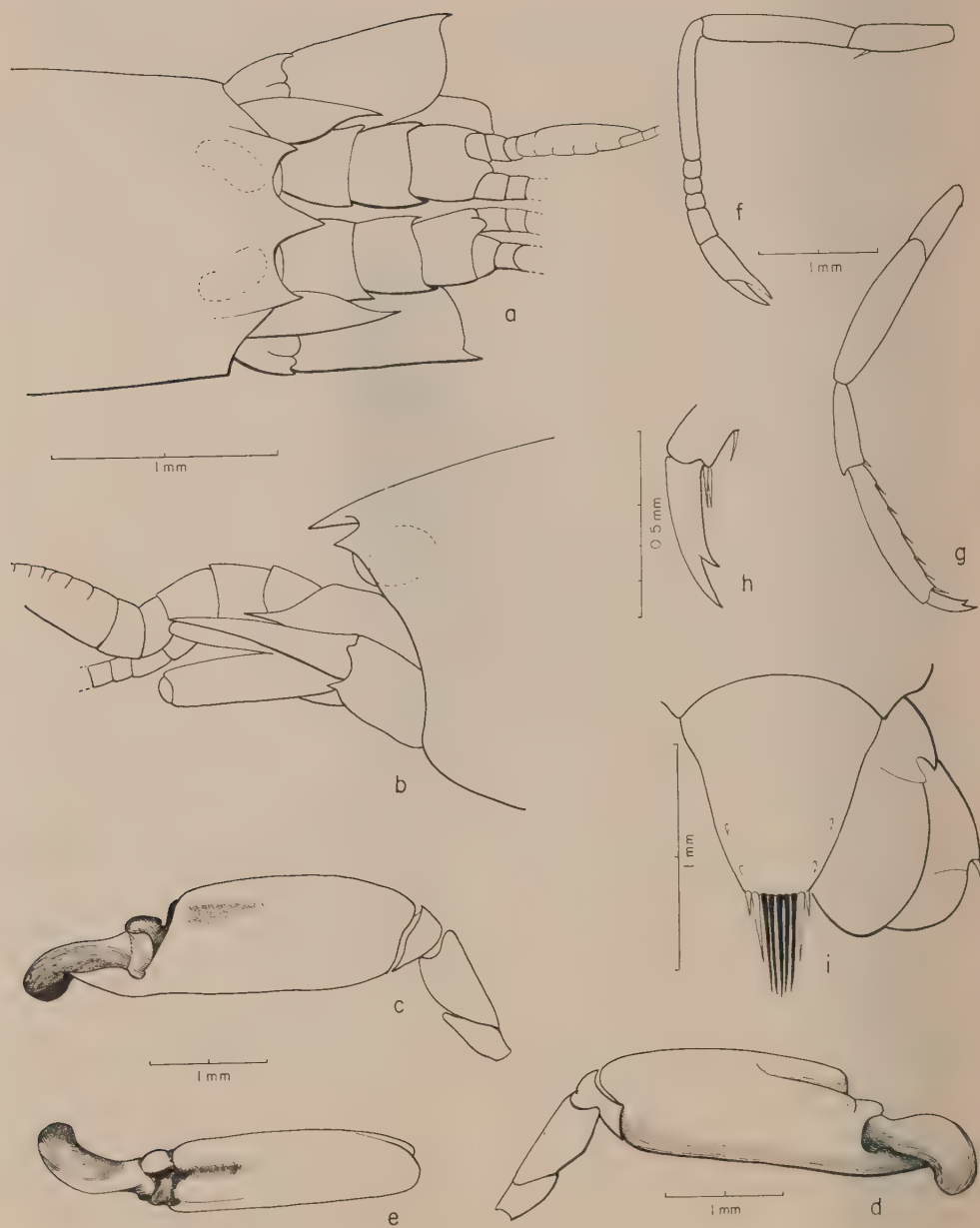


FIG. 3. *Alpheopsis diabolus* sp. nov. *a, b*, Anterior region, dorsal and lateral aspects; *c-e*, large cheliped, lateral, medial and superior aspects; *f*, second leg; *g*, third leg; *h*, third leg, dactylus; *i*, telson and uropod.

and lateral view, but outer margin of eyes visible in both aspects. Pterygostomial angle rounded.

Visible portion of first antennular article 1.3 times length of second article; second article approximately as long as third article and slightly broader than long; stylocerite acute with tip reaching to middle of second article; outer flagellum with basal portion before bifurcation very broad; bifurcation feeble. Basicerite of antennal peduncle with distal lateral tooth; scaphocerite with strong distal lateral tooth, slightly exceeding the length of rounded portion, subequal in length to antennular peduncle; carpocerite slightly longer than scaphocerite.

Merus of large cheliped as broad as inferior margin is long, subequal to maximum length of ischium; ischium and merus unarmed. Carpus short, rounded, with triangular projection on middle of inner margin. Chela compressed, superior and inferior margins rounded. Palm twice as long as ischium and merus combined, slightly over twice as long as broad; outer face with shallow rounded groove extending from dactylar articulation one-third length of palm; superior face marked by deep groove separating two sharp ridges, equal in length to lateral groove. Dactylus articulated to close about 60° to plane of chela, across pointed fixed finger; superior articular surface of propodus carried in rounded prominence beyond crests and grooves of palm to accommodate rotation. Dactylus broad, curved and flattened, without teeth, 0.4 length of palm. Only small tufts of setae located near fingers on chela.

Small cheliped lacking.

Carpus of second legs with ratio: 10: 1.5: 1.5: 1.5: 2.; short articles about as long as broad.

Second legs with ischium unarmed; merus 2.3 times length of ischium and 4.5 times as long as broad, unarmed; carpus 0.5 length of merus, with small movable spine on inferior distal angle; propodus as long as merus, armed with five inferior and two distal slender

spines; dactylus 0.3 length of propodus, with strong accessory tooth on inferior margin.

Pleura of sixth abdominal segment articulated.

Telson short and broad, 3.2 times as long as tip is broad, 3.0 times as broad anteriorly as at tip; tip almost straight, bearing two pair of spines, five heavy setae; longer spines three times as long as shorter, equal in length to breadth of tip of telson; anterior pair of dorsal spinules located about 0.7, posterior pair about 0.85 distance from base of telson, both pairs located near lateral margins. Outer uropod with strong spine at articulation; both uropods longer than telson.

Branchial formula with five pleurobranches, one arthrobranch and eight epipodites.

Eggs few, 0.62×0.36 mm. in diameter.

DISCUSSION: This species plainly belongs to the genus *Alpheopsis* as is shown by the articulated pleopods of the sixth abdominal segment, by the general form of the anterior portion of the carapace and by the branchial formula. The form of the chela is somewhat similar to that of *A. trispinosus* (Stimpson) and *A. chilensis* Coutière (see Coutière, 1899, figs. 228–232).

Within the genus, however, it differs from all other forms except *A. fissipes* Coutière and (?) *A. biunguiculatus* Banner in the presence of biunguiculate dactyli on the third to fifth legs. From *A. fissipes* it differs principally in the presence of extracorneal teeth, the greatly elongate first carpal article of the second leg, and the difference in proportions and armature of the third legs. Similarly, it differs from (?) *A. biunguiculatus* in the extracorneal teeth, the carpus of the second legs, and the armature of the propodus of the third legs; it also differs in the branchial formula and the form of the telson. (In neither of these species are the chelae known.) As far as I have been able to determine, the form of the large chela, with the double grooves and the rotation of the flattened and unarmed dactylus is unique within the genus; however, in many of the species the chelae have not been described.

This specific name refers to the split unguis.

Alpheopsis tetrarthri sp. nov.

Fig. 4

TYPE: A 6.0 mm. female collected from a head of dead coral at Loc. 2 by Preston E. Cloud, Jr., 28 April 1949. Type to be deposited in the U. S. National Museum.

DESCRIPTION: Anterior carapace projecting as a broad curved collar, reaching almost to end of first article of antennular peduncle; anterior margin uniformly curved; dorsal surface smooth, without ridges or bosses. Rostrum small, triangular in dorsal view, tip reaching about to end of first third of second antennular article; in lateral view appears to be composed of a lamella hanging ventral to carapace proper, tip strongly depressed. Ptery-

gostomial angle projecting as acute spine; no other spines of anterior carapace developed.

Cornea of eyes large, entirely concealed from dorsal and lateral view by carapace.

Antennular peduncle short, heavy, with second article about as broad as long, approximately as long as third article; first article barely visible under projecting edge of carapace. Stylocerite acute, reaching to middle of second article, slightly beyond tip of rostrum. Flagella of usual size, about twice as long as peduncle. External flagellum with broad base bearing tuft of long bristles, but without trace of bifurcation.

Basicerite of antennal peduncle without tooth. Scaphocerite broad, well developed, with lateral spine small, reaching anterior tip of curved portion; tip of scaphocerite definitely exceeding antennular peduncle in

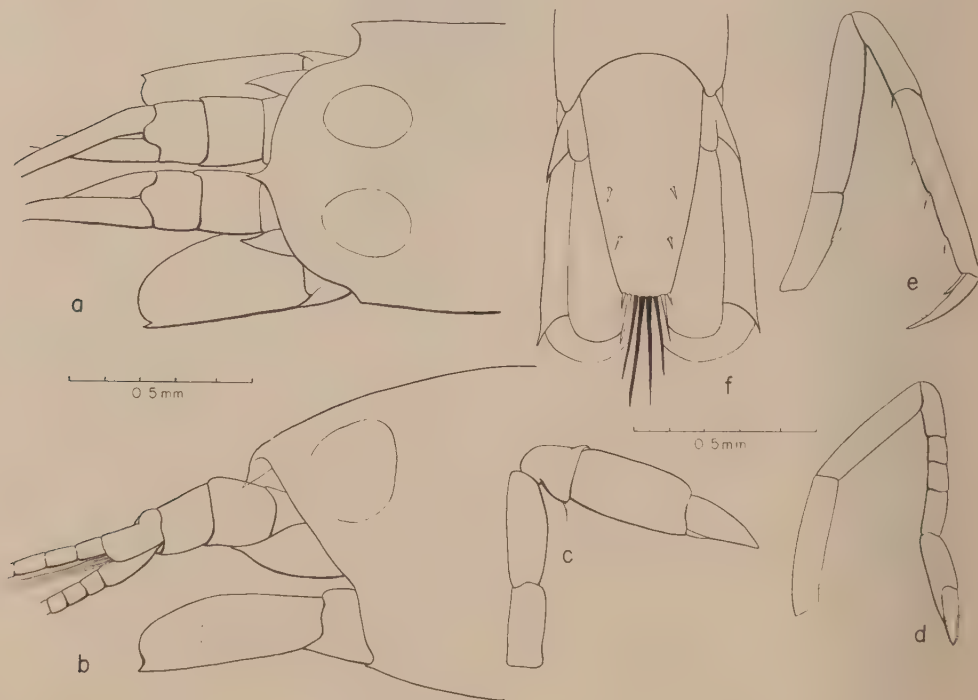


FIG. 4. *Alpheopsis tetrarthri* sp. nov. a, b, Anterior region, dorsal and lateral views (outline of distal portion of carapocerite dotted in b); c, cheliped; d, second leg; e, third leg; f, telson and uropods.

length. Carpocerite short, reaching only slightly beyond end of second antennular article.

Mouthparts not dissected.

One of first chelipeds lost. Chela of leg remaining small, as long as ischium and merus combined; palm about twice as long as broad, 1.5 times as long as tapering slender fingers. Carpus as broad as long, slightly cyanthiform distally. Merus rounded-triangular in section, about 2.5 times as long as broad. Ischium 0.7 as long as merus, of same width.

Second legs with carpus of only four articles with ratio: 10: 5: 7: 9. Chela relatively large, as long as merus.

Third, fourth, fifth legs similar. On fourth leg ischium 0.6 as long as merus, bearing movable spine; merus five times as long as broad, unarmed; carpus half as long as merus; propodus slightly longer than merus, bearing three slender spines on inferior margin, one distally; dactylus half as long as merus, slender, tapering to fine tip.

Pleura of sixth abdominal segment articulated.

Telson twice as long as broad anteriorly, with tip 0.4 as broad as base; two pairs of dorsal spines, anterior located at half length of telson, posterior midway between anterior pair and tip; tip shallowly arcuate, bearing four spines, longer pair as long as tip of telson is broad, four heavy setae. Uropods of usual form.

Branchiae difficult to discern, but apparently with five pleurobranchs, arthrobranchs either rudimentary or entirely lacking; seven or possibly eight epipodites.

DISCUSSION: Unfortunately this species is represented by a single defective specimen, possibly also immature. It appears to belong to the genus *Alpheopsis*. The form of the carapace and rostrum are similar to that of *Alpheopsis equalis* except that the carapace extends much farther forward and the rostrum is relatively smaller; the antennular and antennal peduncles are of the same general form

as *A. equalis* but of slightly different proportions; the small chela is almost identical to the small chela of *A. equalis*, as are the third and fourth legs; the telson and uropods, and the articulated sixth pleopods of the abdomen are also similar. The principal differences between *tetrarthri* and the other species of the genus are the presence of four articles in the carpus of the second leg in this species whereas in the others there are either three articles (*A. idiocarpus* Coutière) or five and a difference in the branchial formula which in this species is apparently 5-0-7, instead of 5-1-6 or 5-1-8. (It should be noted that (?) *Alpheopsis biunguiculus* Banner (1953: 19) has a rudimentary arthrobranch and only seven epipodites.) The species is assigned to this genus in spite of these possible fundamental differences because it has been accepted already that the number of articles in the carpus is not fixed in this genus, and because I could not determine the branchial formula to my satisfaction without tearing this unique specimen apart. Without the large chela, even if all the other characteristics were in complete agreement, any generic identification would be tentative.

Within the genus *Alpheopsis* this species can be separated readily from all other species by the presence of only four articles in the carpus of the second leg and by the extreme prolongation of the anterior margin of the carapace. Other minor differences occur between *tetrarthri* and the other species such as the proportions of the stylocerite and antennular peduncle; the proportions of the scaphocerite and antennal peduncle; the simple or bifid dactylus of the third legs; and the proportions of the telson.

SYNALPHEUS Bate
Neomeris group

Synalpheus charon obscurus, subsp. nov.

Fig. 5

Alpheus charon Heller, K. Akad. Wiss. Wien, Sitzungber. 44: 272, 1861.

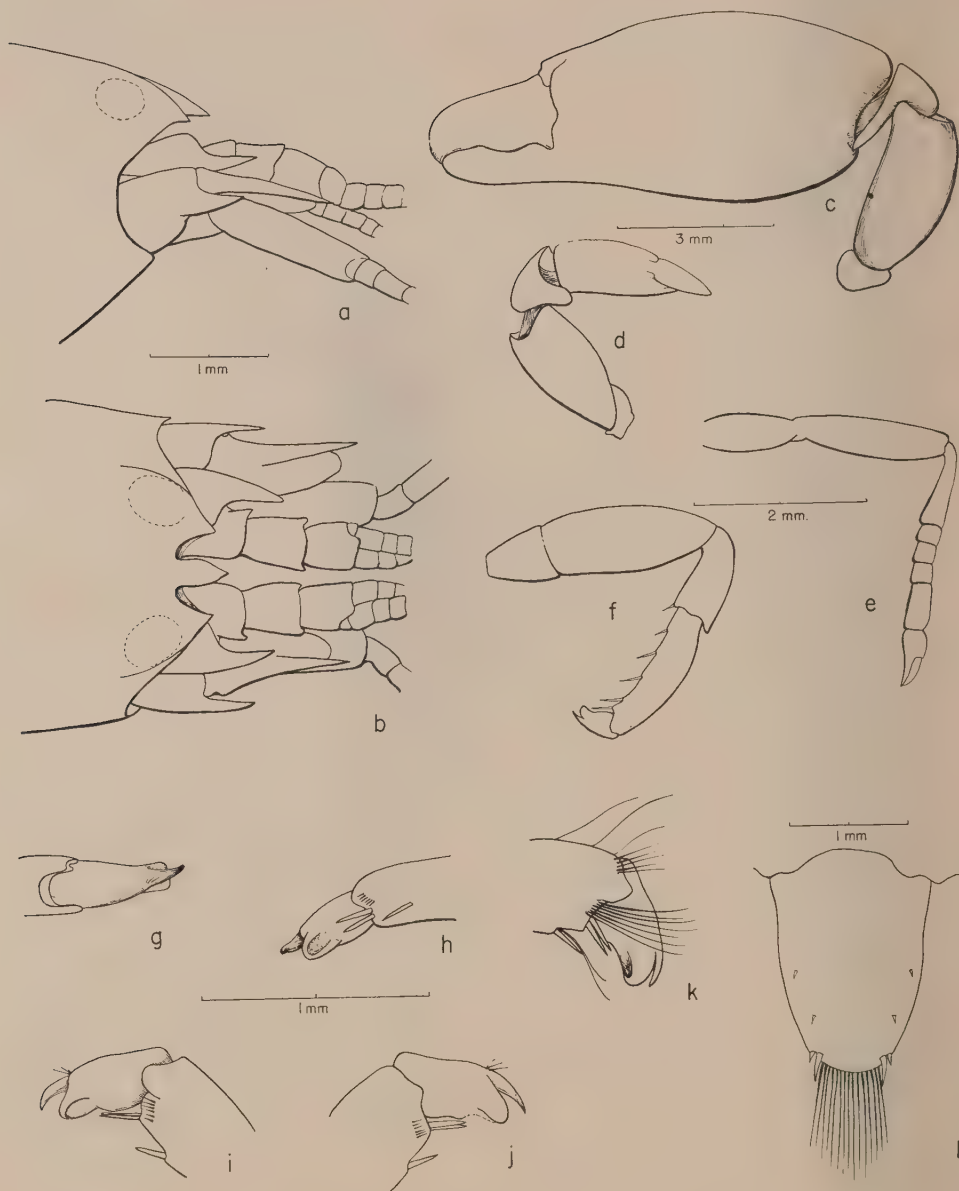


FIG. 5. *Synalpheus charon obscurus* subsp. nov. *a, b*, Anterior region, dorsal and lateral aspects; *c*, large cheliped; *d*, small cheliped; *e*, second leg; *f*, third leg; *g, h, i, j*, dactylus, third leg, superior, inferior, medial or anterior, and lateral or posterior aspects; *k*, dactylus, fourth leg; *l*, telson.

TYPES: Holotype a 13.5 mm. ovigerous female, collected by A. H. Banner from the reef flat on the S. E. side of Unai Obyan, Saipan, 25 December 1944; allotype, a 9.3 mm. male from the same location; paratypes, 14 other specimens from three collections, A. H. Banner, collector.

DESCRIPTION: Body heavy, compact. Rostrum with basal portion parallel sided, slightly over distal third tapering, tip acute, not reaching end of first antennular article. Orbital hoods acuminate, tips of orbital teeth not reaching end of rostrum.

First and second articles of antennular peduncle subequal in length, third slightly shorter. Stylocerite heavy, tip reaching to middle of second antennular article. Lateral spine of basicerite heavy, slightly shorter than stylocerite. Lateral tooth of scaphocerite as long as antennular peduncle, definitely longer than the squamous flattened portion.

Merus of large cheliped unarmed, slightly curved, twice as long as broad. Chela 2.5 times as long as broad, with heavy fingers occupying distal 0.28; superolateral margin of palm continued over dactylar articulation as slight rounded tooth. Merus of small cheliped likewise unarmed; carpus slightly greater in diameter than palm of chela. Chela small, 0.3 the length of the large chela, 0.3 times as broad as long, with fingers occupying distal 0.4.

Carpal articles of second legs with ratio: 10:2.3:2.7:2.7:6.2.

Ischium of third legs unarmed, about one third as long as merus; merus unarmed, 2.4 times as long as broad; carpus half as long as merus, armed with single movable spine on inferodistal angle; propodus 0.8 as long as merus, bearing four inferior and two distal spines; dactylus heavy, with superior unguis simple, tapering, inferior unguis massive, concave on inferior surface; dactylus may or may not be flanked with long setae arising from distal end of propodus.

Telson 2.8 times as long as posterior margin is broad, and 2.0 times as wide anteriorly as

posteriorly; margins without uniform taper, but concave in anterior third, convex in middle third and almost straight (but not parallel) in distal third. Dorsal spinules small.

Eggs numerous, 0.41×0.63 in diameter.

Male similar to female in form and proportions.

DISCUSSION: This subspecies can be separated from the typical subspecies, *S. charon charon*, by the following characteristics: 1, The rostrum is parallel-sided in at least the basal half rather than uniformly tapered. 2, The meri of the third legs, are 2.4 instead of 3.0 times as long as broad. 3, The superior unguis of the dactyli of the third legs is not as broad basally and has a uniform taper to the tip rather than with a broad basal plate which is abruptly narrowed to a curved tip. Otherwise the two varieties are almost identical aside from minor and insignificant differences in the proportions of the second legs, telson, etc.

Because of the unique concavity of the dactyls of the posterior legs, found only in *S. charon* in this genus, it was considered that this form is merely a subspecific modification. On Saipan no true *S. charon charon* were collected; however, in the Gilbert Islands both subspecies were found (to be reported upon in a later publication).

Synalpheus paraneomeris Coutière

Fig. 6

Synalpheus paraneomeris Coutière, Fauna and Geog. Mald. and Laccad. 2(4): 872, pl. 71, fig. 7, 1905.

LOCALITIES: Banner, 64 specimens in 6 collections; Cloud, 19 specimens at Loc. D-6, 8 at Loc. 6.

DISCUSSION: The variation in this species has been discussed by Coutière (*loc. cit.*) and Banner (1953: 40 *et seq.*). The great variation noticed in the Hawaiian specimens is duplicated and even exceeded in the specimens from Saipan. Like the Hawaiian specimens, they vary in the length of the rostrum relative

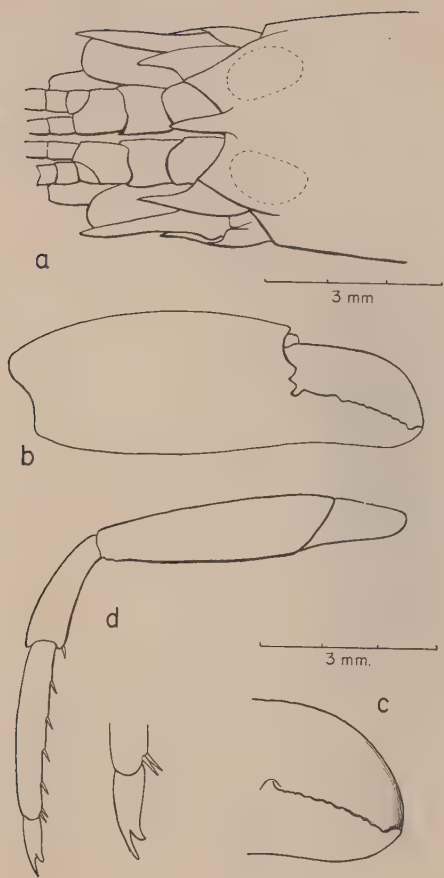


FIG. 6. *Synalpheus paraneomeris* Coutière. Aberrant specimen. *a*, Anterior region, dorsal aspect, showing asymmetry in orbital hoods; *b*, large chela, lateral aspect; *c*, large chela, fingers, showing details of teeth; *d*, third leg; *e*, third leg, dactylus enlarged.

to the orbital teeth and antennular peduncle, in the antennular peduncle, in the basicerite and scaphocerite of the antennal peduncle, in the large cheliped, in the relative lengths of the carpal articles of the second legs, in the dactyli of the third legs, in the general proportions of the telson. In addition, variations occur in the relative length of the carpocerite, which varies from only slightly longer to considerably longer than the scaphocerite, and in the rostrum and in the large cheliped.

In the 19 specimens from Cloud's collec-

tion D-6 the length of the rostrum relative to the lengths of the orbital hoods, and its relative breadth were measured. (In one specimen the rostrum was entirely lacking, a condition interpreted as the result of an accident of heredity or environment.) The ratio of rostral length to orbital hood length ranged from 1:1 to 1.6:1, with the following distribution:

ROSTRAL LENGTH ÷ LENGTH ORBITAL HOOD	SPECIMENS
1.0.....	3
1.1.....	4
1.2.....	4
1.3.....	2
1.4.....	1
1.5.....	0
1.6.....	4

ROSTRAL LENGTH ÷ ROSTRAL WIDTH AT BASE	SPECIMENS
1.5.....	3
2.0-2.9.....	6
3.0-3.9.....	7
4.0-4.5.....	2

In a collection of 25 specimens made by the author, a series of specimens in which all chelae were intact, the relative lengths of the fingers were measured, and these measurements correlated with the sex of the specimens and are tabulated below:

CHELA LENGTH ÷ FINGER LENGTH	SPECIMENS	
	Male	Female
2.9.....	2	
3.0.....	2	
3.1.....		
3.2.....	1	1 (?)
3.3.....		
3.4.....		
3.5.....	1	2
3.6.....		3
3.7.....		4
3.8.....		3
3.9.....		1
4.0.....	1 (?)	2
4.1.....		
4.2.....		2

The interpretation of this second series of variations is simple: the length of the fingers relative to the chela is a sexually dimorphic

characteristic. (It should be remarked that males in other samples from Saipan had a ratio as low as 2.8:1.) The interpretation of the variations in the rostrum is more difficult, especially in view of the four specimens which seem so different in having the rostrum 1.6 times as long as the orbital hoods. However, these four specimens did not bear correlating difference in their other characteristics; for example, their rostral width ratios were 1.6, 1.6, 3.3, and 4.3, or, in words, two had very broad rostrums, one average, and one very narrow. So it would appear that this, too, was merely a variation.

In one collection there are two males with the chela:finger ratio of 3.0:1 in which the cutting edge of the fixed finger had shallow denticulations. One of these specimens is shown in Figure 6. The specimens are within the range of variation for the species, although the unguis of the dactylus of the third legs is a bit narrower and more parallel-sided than is usual for the species.

This species is the most perplexing I have encountered. If such wide variation is found here, why do other species appear to be so constant? Then, should not this be interpreted as more than one species? If the variations were discontinuous, or even if the variations were continuous, but their continuity could be established only by samples from separate localities or habitats—if, for example, those with the short rostrums were only found in the Marianas, those with long rostrums in Hawaii, and those in the intermediate condition were found in Micronesia—then descriptions of separate subspecies or species would be justified. But such separation seems unjustified when the range of variation is found in one habitat and in specimens collected at one time. If such variation is found in *S. paraneomeris*, should not similar variation be looked for in other species which are separated by small, but discrete, differences? For example, *S. biunguiculatus* (Stimpson) (as redescribed by Banner, 1953: 33) basically is separated from this species by the relatively

smaller lower unguis of the dactylus of the third leg—could not this, too, be an inherent variation that may be ignored by a breeding population? I fear that the answer to this fundamental question can be arrived at only by the almost impossible task of raising the shrimp through several generations.

Coutierei Group

Synalpheus coutierei *exilipes* Coutière

Fig. 7

Synalpheus biunguiculatus var. *exilipes* Coutière, Fauna and Geog. Mald. and Laccad. 2(4): 874, pl. 71, fig. 10, 1905. [*nec. Alpheus biunguiculatus* Stimpson, Acad. Nat. Sci., Phila., Proc. 1860: 31] *Synalpheus coutierei* Banner, Pacific Sci. 7(1): 36, 1953.

LOCALITY: Cloud, an 8.5 mm. ovigerous female collected at Loc. 6.

DESCRIPTION: Rostrum narrow, tapering, suddenly acute at tip, tip reaching almost to end of first antennular article. Orbital teeth narrow, tapering, slightly shorter than rostrum; orbital hoods slightly inflated anteriorly.

Second antennular article 1.4 times as long as broad, or as long as first article, and one third longer than third article. Stylocerite as long as first antennular article and as lateral spine of basicerite. Basicerite with superior lateral angle projecting as small acute tooth. Scaphocerite as long as antennular peduncle. Carpocerite 6.5 times as long as broad in lateral view, tip reaching beyond end of antennular peduncle.

Large chela of usual shape for genus, 2.7 times as long as broad, with fingers occupying distal 0.2. Merus twice as long as broad, superior margin slightly arcuate and terminating in feeble tooth. Small chela with fingers tapering, occupying distal 0.4.

First carpal article of second leg equal to the sum of the lengths of the four following; second, third, and fourth articles subequal;

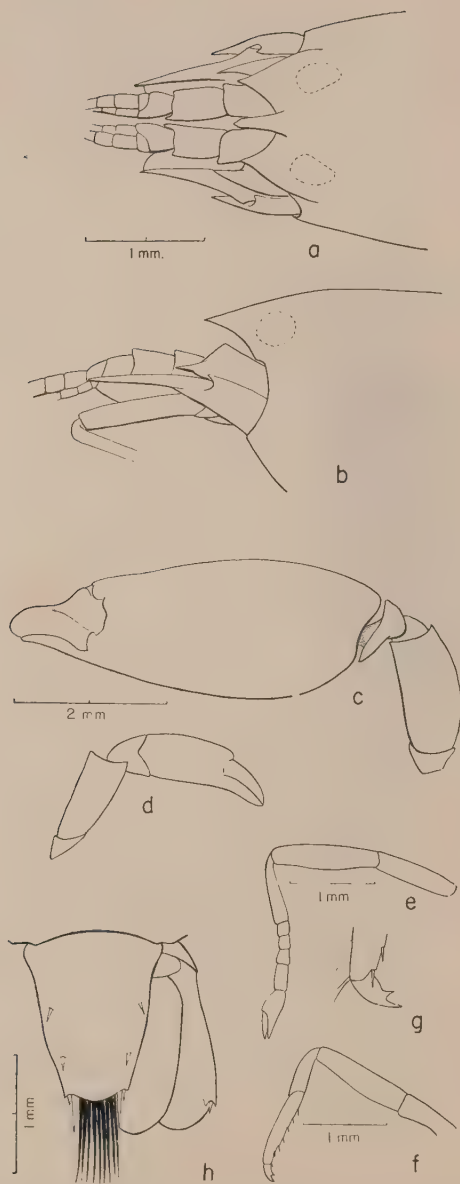


FIG. 7. *Synalpheus coutierei exilipes* Coutière. a, b, Anterior region, dorsal and lateral aspects; c, large cheliped; d, small cheliped; e, second leg; f, third leg, g, third leg, dactylus; h, telson and uropods.

fifth article slightly shorter than the lengths third and fourth combined.

Merus of third legs unarmed, tapering dis-

tally, 4.0 times as long as broad. Carpus 0.38 as long as merus, with superior margin terminated by tooth. Propodus 0.8 as long as merus, bearing six inferior and two terminal weak spines. Dactylus about 0.25 as long as of propodus, heavy, with superior unguis thin, curved and acute, inferior unguis at about 90° to inferior margin of dactyl, triangular, acute and broader at base than superior unguis.

Telson 2.7 times as long as posterior margin is broad, 2.2 times as broad anteriorly as posteriorly; lateral margins as shown in Figure 7b; posteriolateral angles slightly projecting and acute; posterior margin arcuate. Anterior pair of dorsal spinules slightly before the middle, posterior pair 0.8 of length posterior from base.

DISCUSSION: This specimen shows a series of differences from Coutière's subspecies (or variety). The rostrum and the orbital teeth are slightly shorter, the first antennular article is slightly longer, the lateral spines of the stylocerite and the basicerite are slightly shorter. Coutière did not describe the large and small chelae, but if the large chela bore a tooth as did his *S. biunguiculatus* (op. cit., fig. 8a), there, too, lies a difference. However, the proportions of the third legs are almost exactly the same with the depicted dactyli varying on either side of the condition found here.

Certainly the two forms are not identical, but they are so similar that in light of the variation in *S. paraneomeris* Coutière, more importance should be attached to the slight differences. However, it is possible that if there were a series of specimens available the differences would be found to be constant enough to consider this as a distinct subspecies.

Synalpheus anceps sp. nov.

Fig. 8

TYPES: Holotype, an ovigerous 9.5 mm. female, collected from Saipan by A. H. Banner. Allotype, a 7.3 mm. male; paratypes, 13 specimens of both sexes, all collected by

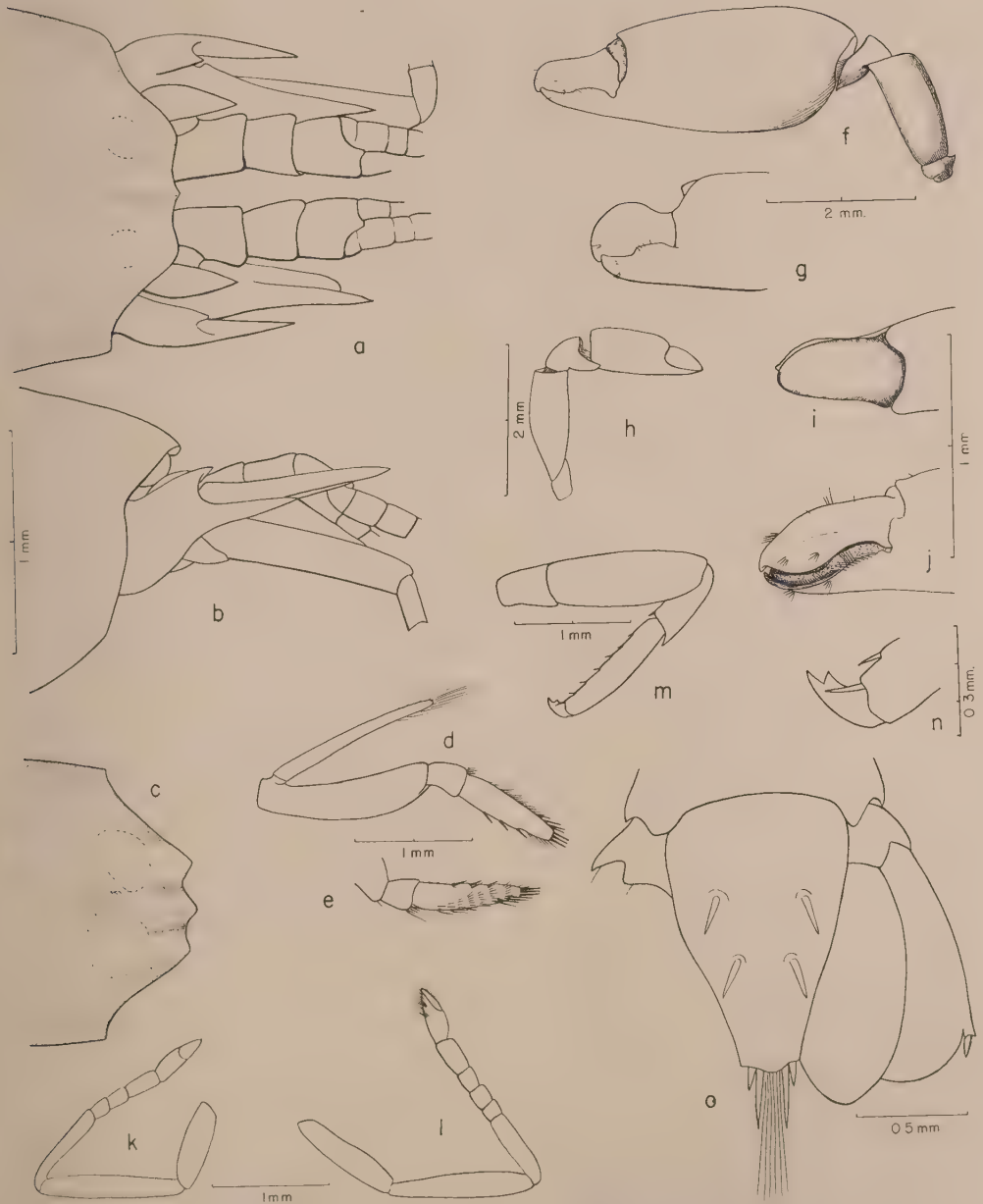


FIG. 8. *Synalpheus anceps* sp. nov. a, b, Anterior region, dorsal and lateral aspects; c, anterior region, another specimen; d, e, third maxilliped; f, g, large cheliped; h, small cheliped; i, spatulate dactylus of small cheliped, type; j, same, paratype female; k, second leg, right side; l, same, left side; m, third leg; n, third leg, dactylus; o, telson and uropod.

Banner at three different times. Types to be deposited in the U. S. National Museum.

DESCRIPTION: Anterior portion of carapace almost truncate anterior to eyes, rostrum produced into very slight angle; in lateral view anterior margin depressed; orbital hoods low but slightly higher than median area of carapace; rostral carina short, low and rounded. Pterygostomial angle of carapace slightly projecting but rounded; cardiac notch present. Cornea of eyes visible under carapace in lateral view.

Second antennular article 0.8 as long as broad, 0.7 as long as visible portion of first and 0.8 as long as third article. Stylocerite slightly shorter than basal article, acute but with lateral spine poorly developed. Outer flagellum with secondary ramus consisting of two articles; both flagella only slightly longer than base.

Basicerite with superior tooth heavy but short, subacute; lateral tooth heavy, long and acute, reaching to end of second antennular article. Scaphocerite with heavy lateral spine reaching beyond end of antennular peduncle, 1.2 times as long as the narrow squamous portion. Carpocerite longer, slender, reaching considerably beyond end of scaphocerite.

Third maxillipeds of normal form, with inner face of terminal article bearing numerous bristles and movable spinules.

Merus of large cheliped triangular, with definite margins between the faces, outer face 2.3 times as long as broad; superior distal and inferior internal angles unarmed. Carpus expanded and short. Chela 2.4 times as long as broad, 3.3 times as long as fingers, rounded in side view, laterally slightly compressed; short, heavy, rounded tooth above dactylar articulation. Dactylus heavy, compressed, with distal margin strongly arcuate; dactylus with usual "plunger" and without adhesive plaques. Very light scattered setae on both fingers.

Small cheliped with merus as long as that of large chela, but more slender. Carpus hemispherical but with inferior projecting flange

that covers base of chela. Chela as long as merus, 1.6 times as long as broad, with fingers occupying distal third. Dactylus of peculiar shape, rounded on superior surface and rounded distally, with tip bearing strong, acute tooth at about 90° to fixed finger. Fixed finger broadened to meet dactylus and with tip projecting as two rounded teeth which articulate with dactylar tooth.

Second legs with ischium and merus heavy; carpus of right leg with four articles (ratio 10:1.5:1.7:2.7), that of the left with five (ratio 10:1.2:1.5:1.5:2.7).

Ischium of third legs unarmed. Merus 3.0 times as long as broad, unarmed. Carpus 0.4 as long as merus, armed with heavy terminal tooth on superior margin and small movable terminal spine on inferior margin. Propodus heavy, 5 times as long as broad, 0.8 as long as merus, armed with six slight spines on inferior margin. Dactylus biunguiculate, superior spine heavy and curved, inferior spine shorter, heavy and at about 90° to inferior margin.

Abdomen very broad, shallow, pleura expanded and second pleura bearing deposit of fat. Pleopods long and broad.

Uropods of usual form, outer bearing single distal lateral spine. Telson 5 times as long as posterior margin is broad, base 3.3 times as broad as tip; inner pair of spines of tip as long as tip is broad; dorsal spines about 0.7 as long as inner distal spines, located at 0.3 and 0.6 of the length posterior from articulation.

Nine eggs, 0.73×1.13 mm. in diameter.

Branchial formula: 5-1-2.

Allotype not exhibiting sexual dimorphism in any character except abdomen, which is less expanded, with shorter pleura and pleopods.

DISCUSSION: This series of 15 specimens exhibits variation in a number of characteristics. In some the anterior carapace projects relatively further (Fig. 8c), the truncate portion is narrower in dorsal view and less depressed in lateral view, and the orbital projections and rostrum are more pronounced,

also the rostral carina is slightly higher but still neither strong nor sharp. In one specimen, the front of the carapace is straight, showing no vestige of either the orbital teeth or the rostrum. In general the larger specimens have the straighter front. The pterygostomial angle also varies in the amount of projection but in no case is it definitely angular.

In all specimens the eyes are fully concealed in dorsal view, but with part of the cornea visible in lateral view, as is shown in Figure 8*b*.

No great variation has been noted in the antennular peduncle. However, the superior tooth of the basicerite is stronger and more acute in some specimens and its tip may reach almost as far forward as does the stylocerite. In many the flattened portion of the scaphocerite is more reduced, and in several the lateral spine of the scaphocerite does not reach past the middle of the third antennular article. The carpoperite is always markedly longer than the antennular peduncle.

On the large cheliped the distal superior margin of the merus may project to form a slight, rounded tooth and the inferior external margin in some specimens projects slightly more than it does on the type. The tooth above the dactylar articulation may be either more or less well developed than on type. The small cheliped does not show marked variations.

All specimens except one had four articles to the carpus of the second legs, and that one, like the type, had five articles in the carpus of the one second leg remaining on the specimen.

The proportions of the telson varied somewhat, and the dorsal spinules varied from about half the length to much larger than those in the type; in one specimen the posterior pair reach almost to the tip of the telson.

In the ovigerous females the size of the eggs was relatively constant, depending upon their maturity, but the number varied from five to fifteen.

Although the number of articles of the carpus, the almost flatly truncate anterior margin of the carapace, and the exposure of the cornea of the eyes in lateral view is unlike any other species of the genus *Synalpheus*, this species has been placed in this genus for the following reasons: 1, The anterior teeth of the carapace approaches this condition in some of the species of the genus, e.g., *S. tanneri* Coutière (1909: 77). 2, The general form of the antennular and antennal peduncles of this species is definitely like other species of *Synalpheus*. 3, The pterygostomial angle of this species at least approaches the usual form for the genus. 4, The large and small chelae are like other species of the genus, both in general form and in the presence of the plunger on the dactylus of the large chela and in the absence of adhesive plaques on the propodus and dactylus. Moreover, the form of the small chela is almost identical to that of *S. pescadorensis* Coutière (1905: 887). 5, The form of the third legs is similar to other species of the genus and the form of the telson is often found in the genus. 6, The branchial formula is that of *Synalpheus*.

The essential differences, then, between this and other members of the genus are in the four articles to the carpus of the third legs—which is variable in this species and has been found to vary in other species of this genus (Coutière, 1909: 20; Banner, 1953: 29), and in the exposure of the eyes, which may be merely the result of the reduction of the anteriorly projecting portion of the carapace.

Within the genus this species appears to fall in the old "Biunguiculatus" group, now better called the Coutièrei group (Banner, 1953: 37). Within this group it is related to those with a subspatulate dactylus of the small cheliped, but it can easily be separated by the extreme reduction of the orbital teeth and rostrum, by the lateral exposure of the cornea, and by the condition of the carpus of the second legs.

The name does not refer to any "two-faced" condition but rather to variation in the num-

ber of secondary articles in the carpus of the second legs.

ALPHEUS Fabricius
Megacheles group

Alpheus tuthilli (Banner)

Fig. 9

Crangon tuthilli Banner, Pacific Sci. 7(1): 63, fig. 19, 1953.

LOCALITY: Banner, one specimen, Saipan.

DISCUSSION: This specimen, a 16 mm. female, agrees in all characteristics with the specimen described from Hawaii except that the orbital teeth and lateral spine of the basicerite are slightly longer when compared to the rostrum.

The specimen has intact the small chela which was lost in the type specimen. In it the merus is 3 times as long as broad and 0.5 as long as the entire chela; it bears no superior spines, but the inferior internal margin bears 14 short movable spines and terminates in a small acute tooth. The ischium bears 5 similar spines. The chela is about 5 times as long as broad (the palm proper twice as long as broad), with the fingers 0.55 as long as the chela. The fingers are long and thin, only slightly curved, and have crossing tips. The

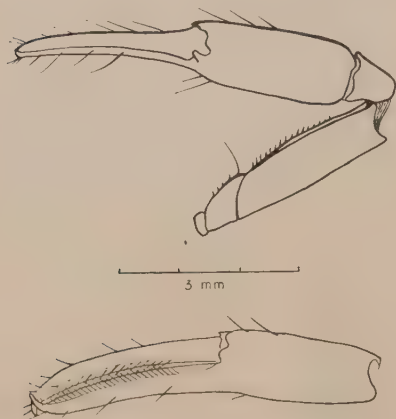


FIG. 9. *Alpheus tuthilli* (Banner). Small chela, female.

opposing faces of the fingers produced as cutting edges that are each flanked on the inner side by a regular row of short stiff setae. The chela bears only occasional long setae.

Alpheus species 1

LOCALITY: Banner, one specimen, Saipan.

DISCUSSION: This specimen without chelae belongs to a new species of the Megacheles group, wherein it is related to the *A. bailstonei* Coutière complex. Because the specimen is incomplete, the description and name will be deferred until a subsequent publication when a more complete specimen will be described.

Alpheus oahuensis (Banner)

Crangon oahuensis Banner, Pacific Sci. 7(1): 64, fig. 20, 1953.

LOCALITY: Banner, 2 specimens in one collection, Saipan.

DISCUSSION: These two specimens, a male and a female, differ in only two ways from the type described from shallow water in Hawaii. The lateral spine of the basicerite is longer and more acute, and the dactylus of the large chela, instead of being thin and crested in the middle and bulbous on the end, is relatively thicker in the middle and not distally expanded. The latter difference may be of significance, but inasmuch as the specimens are otherwise so similar, even to the opposing ridges of the fingers of the small chela, the specimens are assigned to this species.

Alpheus collumianus Stimpson

Alpheus collumianus Stimpson, Acad. Nat. Sci. Phila., Proc., 12: 30, 1860.

Alpheus collumianus probabilis subsp. nov.
Fig. 10

Three variants of this species occur in the present collections and because of the constancy of the differences exhibited are described as subspecies.

TYPES: Holotype, an ovigerous female 15

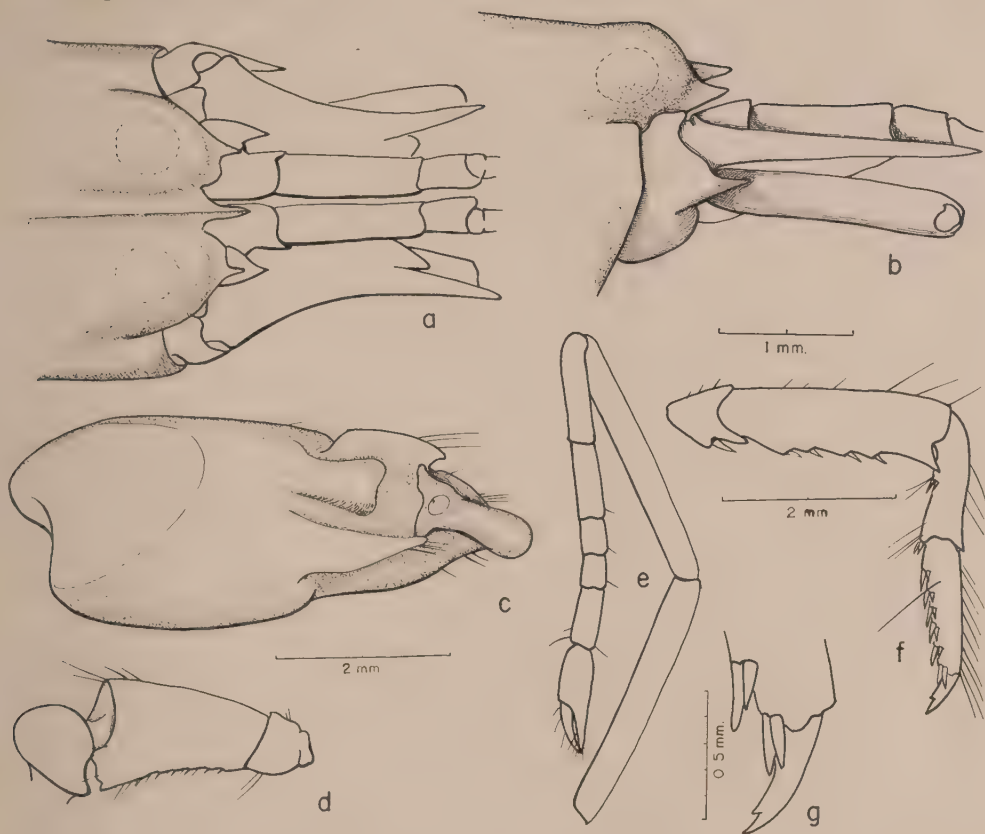


FIG. 10. *Alpheus collumianus probabilis* subsp. nov. a, b, Anterior region, dorsal and lateral aspects; c, large chela; d, large cheliped, merus; e, second leg; f, third leg; g, third leg, dactylus.

mm. long, collected by Preston E. Cloud, Jr., from Loc. C-7a, 13 May 1949. Paratypes: 1 specimen each from Cloud's localities A-7 and C-7a (10 April 1949). All types to be deposited in the U. S. National Museum.

DESCRIPTION: Rostrum acute, short, reaching 0.7 of visible portion of first antennular article, about twice as long as broad at base; depressed in lateral view so that tip is only slightly higher than orbital teeth. Rostral carina strong, narrowly rounded, extending posteriorly to orbital hoods, but lower than orbital hoods in lateral view. Orbital hoods inflated, rounded, and bearing short acute orbital teeth. Margin of carapace between orbital teeth and rostral base dorsoventrally flattened and expanded to form extended area

in front of anteromedial portion of orbital hoods, base of rostrum demarked from this area by deep rounded indentations. Orbitorostral grooves deep but rounded, extending to posterior portion of orbital hoods.

Antennules with second article about twice as long as first and three times as long as third article, four times as long as broad. Stylocerite with well-developed spine reaching almost to end of first antennular article. Scaphocerite longer than antennular peduncle, laterally strongly concave, squamous portion reduced, reaching only to end of second antennular article. Carpocerite as long as antennular peduncle. Basicerite with strong lateral spine, tip reaching beyond end of first antennular article.

Large chela heavy, compressed, 2.4 times as long as broad, with dactylus slightly over 0.2 as long as the entire chela. Superior crest distal to transverse groove strong, narrow, ending in a strong tooth, proximal to transverse groove indistinct. Plaque crest heavy and rounded; superior and palmar grooves deep and distinct on distal third of face of palm. Inferior depression deep and sharply delimited; shoulder rounded. (For explanation of terms see Banner, 1953, fig. 17e.) Chela bearing scattered setae. Carpus of usual form. Merus 0.3 as long as chela, 1.4 times as long as internal face is broad at point of maximum width; inferior internal margin bearing six short strong spines and terminating distally in strong acute tooth.

Small chela lacking in all specimens.

Carpal articles of second leg with ratio: 10:8:4:4:6.

Third legs with ischium bearing strong movable spine; merus 3.3 times as long as broad, with inferior margin bearing four strong spines and terminating distally in strong acute tooth; carpus about 0.5 as long as merus, bearing pair of short spines on middle of inferior margin and another pair on inferior distal angle; propodus 0.7 as long as merus, bearing six pairs of short strong spines on inferior margin (including the terminal spines); dactylus biunguiculate, with inferior unguis about 0.3 as long as and smaller at base than distal unguis. Appendage bearing scattered setae.

Telson 2.0 times as broad at base as at tip, 3.3 times as long as tip is broad, with lateral margins almost straight and anterior pair of dorsal spines located at half distance from base to tip.

DISCUSSION: See under *A. collumianus inermis*, below.

A. collumianus medius subsp. nov.

Fig. 11

Crangon collumiana Banner, 1953, Pacific Sci.

7(1): 67, fig. 21.

TYPES: Holotype, a 19 mm. male, collected by A. H. Banner. Paratypes: Banner, 7 specimens from 4 collections. Cloud, 1 specimen at A-7, 3 at D-6, 1 at E-8, 8 at Loc. 6, 1 at Loc. 8.

DESCRIPTION: Rostrum acute, short, reaching half the length of visible portion of first antennular article, about as long as broad at base, only slightly depressed in lateral view. Rostral carina high but broadly rounded, reaching posteriorly to middle of orbital hoods, only slightly lower than orbital hoods in lateral view. Orbital hoods inflated, rounded, and bearing orbital teeth somewhat shorter than rostrum. Margin of carapace between orbital teeth and rostral base dorsoventrally flattened and expanded; base of rostrum demarked from this area by prominent but shallow indentation. Orbitorostral grooves anteriorly deep but disappearing at level of posterior portion of eyes.

Antennular peduncle with second article about 1.5 times as long as first article, 2.0 times as long as third, and 3 times as long as broad, otherwise similar to *A. collumianus probabilis*. Stylocerite also similar, but with spine less pronounced. Basicerite, carpocerite, and scaphocerite as described for *A. c. probabilis*.

Large chela as described for *A. c. probabilis*. Merus 0.2 as long as chela, 1.3 times as long as internal face is broad, inferior internal margin bearing only setae, and terminating in a strong but rounded tooth.

Small chela of male 0.7 as long as large chela, 3.0 times as long as broad, with the curved heavy fingers occupying 0.55 length of chela and somewhat expanded laterally; superior crest present and terminating distally in strong tooth, proximally at transverse groove; palmar crest and associated grooves poorly demarked; shoulder rounded. Carpus with short blunt tooth projecting over base of palm. Merus almost half as long as chela, 2.2 times as long as outer face is broad; inferior internal margin armed only with light setae and terminating in a low rounded lobe. Small chela of female very similar to that of

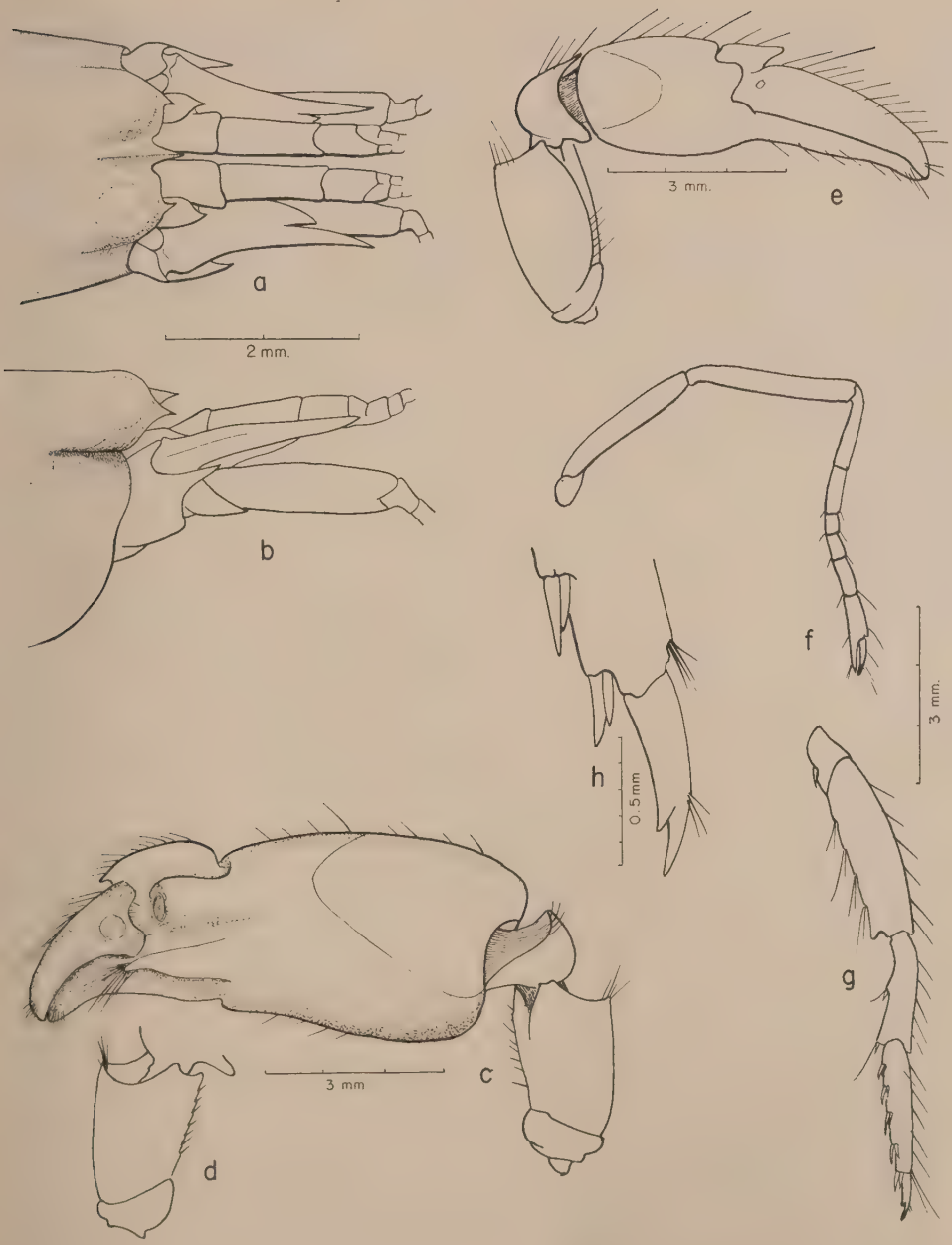


FIG. 11. *Alpheus collumianus medius* subsp. nov. a, b, Anterior region, dorsal and lateral aspects; c, large cheliped; d, large cheliped, merus, medial side; e, small cheliped; f, second leg; g, third leg; h, third leg, dactylus.

male, except somewhat smaller in proportion to large chela, with sculpturing of palm proximal to dactylar articulation less pronounced and dactylus without basal expansion, instead rounded.

Carpal articles of second legs with ratio: 10:8:3:4:5.

Third legs similar to *A. c. probabilis* except that merus is 3.6 times as long as broad, bears setae instead of movable spines on inferior margin, and margin terminates in rounded tooth; distal articles are correspondingly more slender and spines slightly smaller; lower unguis of dactylus slightly larger.

Telson 2.0 times as broad at base as at tip, 2.8 times as long as broad at tip, with anterior pair of dorsal spines slightly anterior to middle.

DISCUSSION: See under *A. collumianus inermis*, below.

A. collumianus inermis subsp. nov.

Fig. 12

TYPES: Holotype, a male 16 mm. long, collected by Preston E. Cloud, Jr. *et al.* from locality D-7. Paratypes: Cloud, 1 specimen at Loc. D-6, 2 specimens from Loc. D-7. Types to be deposited in the U. S. National Museum.

DESCRIPTION: Rostrum short, acute, reaching a little past middle of visible portion of the first antennular article, about as long as broad at the base, tip depressed in lateral view, no higher than front of orbital hoods. Rostral carina only slightly lower than orbital hoods, depressed towards tip, rounded and terminating before middle of eyes. Orbital hoods inflated, rounded, not bearing any teeth in type, but in other specimens bearing very slight acute teeth. Margin of carapace between orbital hoods and rostral base flattened but not extended; base of rostrum demarcated by only very slight broadly rounded indentation. Orbitorostral grooves rather shallow and rounded.

Antennules with second article about 2.0 times as long as first and third articles, 2.5 times as long as broad. Spine of stylocerite

much reduced. Carpocerite and scaphocerite as in *A. collumianus probabilis*; lateral margin of basicerite projecting almost at approximately 90°.

Large chela 2.5 times as long as broad, fingers occupying 0.25 total length; otherwise like *A. c. probabilis*. Merus 0.27 as long as chela, 1.8 times as long as broad, with inferior internal margin armed with setae and terminating in small rounded shoulder.

Small chela (loose in vial, either from type or from 16 mm. female) almost 0.6 as long as large chela, 3.4 times as long as broad, with fingers occupying 0.4 entire length. Sculpturing on palm not marked, but superior crest strong distally and terminating in strong acute tooth. Merus 0.6 as long as chela, 2.3 times as long as broad, with inferior internal margin unarmed.

Carpal articles of second legs with ratio: 10:9:4:4:7.

Third legs with ischium bearing strong spine; merus 3.7 times as long as broad, inferior margin unarmed except for rounded tooth distally; carpus and propodus similar to *A. c. probabilis* except carpus bears neither middle nor terminal spines, and propodal spines are smaller; dactylus with inferior unguis strongly reduced.

Telson similar in form to *A. c. probabilis*, but 2.5 times as broad anteriorly as posteriorly, 3.5 times as long as posterior margin is broad, and with anterior pair of dorsal spinules located 0.4 of length posterior to articulation.

DISCUSSION: The three groups of specimens described above as three subspecies are obviously related. When the inherent minor individual variations are allowed for, they are similar in form of the orbital hoods proper, the antennules and antennae (save for the basicerite and the stylocerite in the last subspecies), in the form of the large chela, in the ratios of the carpal articles of the second legs, in the spiny propodi and biunguiculate dactyli of the third legs, and in the general form of the telsons.

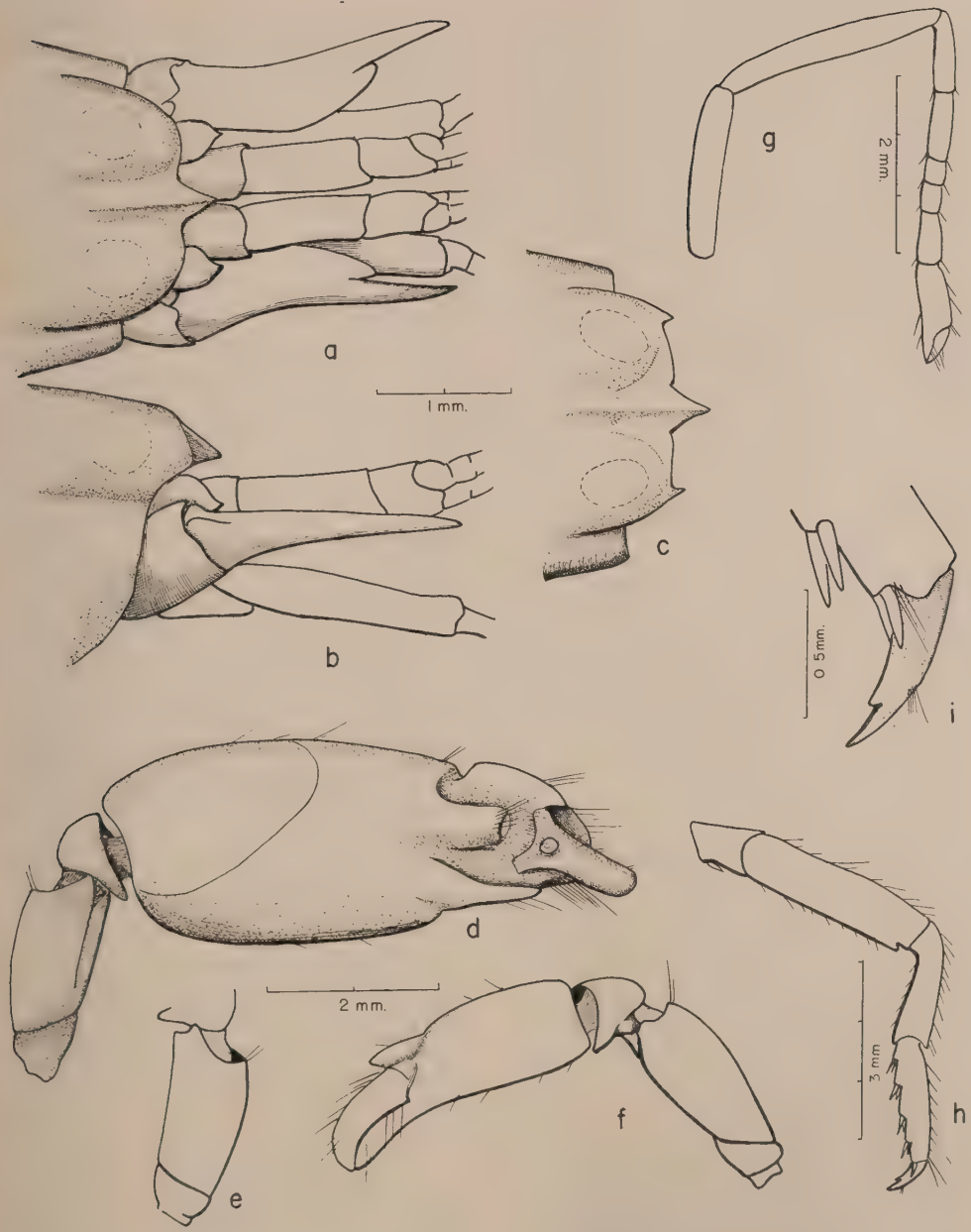


Fig. 12. *Alpheus collumianus inermis* subsp. nov. *a, b*, Anterior region, dorsal and lateral aspects (type); *c*, anterior region (paratype); *d*, large cheliped; *e*, large cheliped, merus, medial aspect; *f*, small cheliped; *g*, second leg; *h*, third leg; *i*, third leg, dactylus.

They differ, however, in the following points:

1. The orbitorostral front. This can best be understood by comparing Figures 10a, 11a, 12a. It should be noted that in three of the four specimens of *A. c. inermis* there are very short orbital teeth, and that *A. c. medius* can be considered a very logical intermediate between the other forms.

2. The stylocerite. Again *A. c. medius* is intermediate between the strong spine of *A. c. probabilis* and the very small spine of *A. c. inermis*.

3. The basicerite. In both *A. c. probabilis* and *A. c. medius* the lateral angle is produced into a strong tooth whereas in *A. c. inermis* it varies from a rounded right angle to a slightly acute angle.

4. The merus of the third legs. *A. c. probabilis* bears four spines and a very strong terminal tooth, *A. c. medius* bears strong bristles corresponding to the spines, and rounded and weaker tooth, and *A. c. inermis* bears scattered weak bristles and a small rounded tooth.

5. The carpus of the third legs. *A. c. probabilis* and *A. c. medius* bear both middle and distal inferior spines (although *A. c. medius* may often lack the middle spines), and *A. c. inermis* bears no spines.

Differences in the proportions of the antennules, antennae, large and small chelae, second and third legs, and telsons probably would not be found to be very significant if larger populations were measured.

In view of the striking similarities yet pronounced differences, it was difficult to decide whether these should be described as separate species or subspecies. There is no way of determining from the specimens and data at hand whether they represent separate ecological groups that would interbreed freely if mixed, or separate co-mingling species that cannot or will not interbreed; however, there is some indication from the collection data that they are separated ecologically, and their

similarities lead me to believe they are merely subspecies.

Without Stimpson's type for comparison—and as far as I have been able to determine, Stimpson's type for this species has been lost like his types for the other alpheids he described—it is difficult to decide which of these, if any, is similar to the specimen for which he gave such a short diagnosis. However, he did state about the third legs, "mero lato, inferne spinuloso et apicem unidentato," which could be applied only to the form described above as *A. collumianus probabilis*. Inasmuch as the original type came from the Bonin Islands, only about 800 miles to the north of Saipan, it is probable that this is identical with the typical subspecies, but because of the distance and the lack of specimens from the Bonins it is inadvisable to assume this to be exactly the same form as would be found there. According to the Copenhagen decisions (paragraph 35, sect. 7) "... the neotype . . . [should come] from as near as possible to that locality [from which the holotype was obtained. . .]," so the description of this subspecies as *A. collumianus collumianus*—which would be essentially the establishment of a neotype—would be of questionable legality.

Without re-examining the specimens it is impossible to be certain to which subspecies the specimens reported by Coutière, de Man and others belong. However, as they did not remark on the differences, it is likely they were *A. collumianus probabilis* (or *A. c. collumianus*). The specimens reported from the Hawaiian Islands by Edmondson and myself definitely belong to *A. c. medius*.

Alpheus deutropus Hilgendorf

Alpheus deutropus Hilgendorf, K. Akad. Wiss. Berlin, Monatsber. 1878: 834.
Crangon deutropus Banner, Pacific Sci. 7(1): 70, fig. 22, 1953.

LOCALITIES: Banner, 1 specimen; Cloud, Loc. 8, 4 specimens. These specimens agree

almost perfectly with the specimens from Hawaii if the range of variation there is considered.

Macrochirus group

Alpheus gracilis var. *simplex* (Banner)

Alpheus gracilis Heller, K. Akad. Wiss. Wien, Sitzungber. 44: 271, Taf. 3, figs. 19–20, 1861.

Crangon gracilis var. *simplex*, Banner, Pacific Sci. 7(1): 75, fig. 25, 1953.

LOCALITY: Banner, 4 specimens from one collection, Saipan.

DISCUSSION: These four specimens agree well with the form described from Hawaii with two exceptions: the dorsal carina, which is lacking in the Hawaiian form and present between the orbital hoods in the typical subspecies, is present but only as a low and obtusely angular ridge in these specimens (it is not delimited, however, by the deep orbitorostral furrows which are found in the typical form); the inferior convexity of the dactylus of the third legs of the Hawaiian form is here developed as a low but flattened protuberance with proximally and distally rounded margins.

Three of the specimens have black spines on the uropods; in the fourth the spines are dark brown.

Alpheus edmondsoni (Banner)

Crangon edmondsoni Banner, Pacific Sci. 7(1): 78, fig. 26, 1953.

LOCALITY: Banner, 2 specimens from one collection, Saipan.

These specimens fall well within the range of variation noted in Hawaii.

Alpheus ventrosus Milne-Edwards

Alpheus ventrosus Milne-Edwards, Histoire Naturelle des Crustacés, 2: 352, 1837.

Alpheus laevis Randall, Acad. Nat. Sci. Phila., Jour. 8(1): 141, 1839.

Alpheus obesomanus Boone, Vanderbilt Mar. Mus., Bul. 6: 135, 1935 [partim].

Crangon ventrosa Banner, Pacific Sci. 7(1): 84, fig. 28, 1953.

LOCALITIES: Banner, 2 specimens in one collection; Cloud, Locs. 6, 8, 9, one specimen each.

DISCUSSION: Two variations are noted in these specimens. First, in several of the smaller specimens, especially in a 15 mm. ovigerous female from Cloud's locality 9, the inter-orbital continuation of the rostrum is high and narrow, almost a rounded carina, instead of flat and broad across the top. In this respect these specimens resemble *A. latipes* (Banner) more closely than they do *A. ventrosus*.

In the two specimens of my own collection, the external spines of the uropods in the 16 mm. female are light brown, and in the accompanying 15 mm. male they are dark brown, almost black. Such dark spines are found in the Macrochirus group and this is often used as a specific characteristic but it has not been remarked upon before in this species.

Alpheus nanus (Banner)

Crangon nanus Banner, Pacific Sci. 7(1): 90, figs. 30, 31, 1953.

LOCALITIES: Banner, 8 specimens in 3 collections; Cloud, locality D-6, 2 specimens.

DISCUSSION: These specimens agree perfectly with those from Hawaii except that about half of these bear up to six weak spinules or short bristles on the inferior internal margins of the meri of the large and small chelipeds.

Alpheus paragracilis (Coutière)

Alpheus paragracilis Coutière, Paris Mus. d'Hist. Nat., Bul. 3(7): 304, 1897b.

Crangon paragracilis Banner, Pacific Sci. 7(1): 96, fig. 33, 1953.

LOCALITY: Cloud, Loc. 6, 2 specimens.

These specimens agree well with those described from Hawaii.

Obesomanus subgroup

Alpheus microstylus (Bate)

= *Betaeus microstylus* Bate, Challenger Repts. 24: 566, pl. 101, fig. 6, 1888.

Alpheus obesomanus de Man, Arch. Naturg. 53: 520, 1888; Abhandl. Senckenb. Naturf. Gesells. 25: 867-869, 1902.

Alpheus malleodigitus Coutière, Les Alpheidae, p. 223, 316 (figs. 270-272, 400) 1899 [nec *A. malleodigitus* (Bate)].

Alpheus microstylus Coutière, Fauna and Geog. Mald. and Laccad. 2: 884, pl. 76, fig. 23, 1905.

LOCALITIES: Banner, 5 specimens in one collection; Cloud, 15 specimens at locality A-5, 4 at FX.

DISCUSSION: The few specimens of this species exhibit some interesting variations. The scale of the antenna is usually similar to that depicted by Coutière (1905) but in several specimens it is shortened, and in one the squamous portion is so reduced that it does not reach to the end of the second antennular article. The merus of the large chela usually bears an obtuse tooth distally on the inner inferior margin, but in some specimens this tooth is acute, and in one small specimen it is reduced to a slight rounded eminence. The ratio of the first two articles of the carpus of the second legs varies from slightly less than 1:3 to more than 1:4. Finally, the propodus of the third legs is armed with five to seven spines instead of only five, as described by Coutière.

Alpheus lutini Coutière

Alpheus lutini Coutière, Fauna and Geog. Mald. and Laccad., 2: 885, pl. 76, fig. 24, 1905; de Man 1911, Siboga Exped. 39a¹: 346, pl. 14, fig. 69 [additional description].

LOCALITIES: Banner, 65 specimens in 8 collections; Cloud, 2 specimens at localities A-7, 3 at C-1, 1 at C-7a (13 May 1949), 6 at D-5.

DISCUSSION: This species is more variable than has been indicated previously, and shows

variation in most of the structures commonly measured. For example, the squamous portion of the scaphocerite, while always poorly developed, may be twice as large in some specimens as in others; the lateral spine of the scaphocerite may equal the antennular peduncle in length, or it may reach only slightly beyond the end of the second antennular article (in one specimen the spine of the left scale reached to the end of the second antennular article, whereas the right reached only to the middle of the same article). Coutière stated that the second legs were 3 times as long as the carapace, whereas in these specimens they vary from about 2 times to more than 3.5 times as long. Similar variations in proportions occur in the chelae and in the third legs.

Except for these variations these specimens agree very well with Coutière's description. At times however, this variation caused difficulty in the use of de Man's key (1911), for while de Man stated that the small chela was less than 3.0 times the length of the fingers (Coutière's ratio was 2.5), it was actually found to be as much as 3.2 times this length.

Alpheus phrygianus Coutière

Alpheus phrygianus Coutière, Fauna and Geog. Mald. and Laccad. 2: 886, pl. 77, fig. 25, 1905.

LOCALITIES: Banner, 2 specimens in one collection; Cloud, 3 specimens at locality A-5, 2 at A-7, 2 at C-1, 3 and 4 at C-7 on 4 April and 13 May 1949, respectively, 2 at D-5, 2 at D-8, 2 at E-7.

DISCUSSION: This species is abundant in the Saipan collections, but few of the specimens are intact, probably in part because most of the specimens died with the long thoracic legs outspread.

In general the specimens agree with Coutière's description of specimens from the Indian Ocean; however, far greater variation is seen in these specimens than was noted by Coutière for his four specimens.

In the younger specimens (less than 10 mm. long) the antennular peduncle is shorter, especially the second article. In the antenna, the spine on the scaphocerite varies from about two-thirds the length of the second antennular article (on an 8 mm. specimen) to less than one-third its length on mature specimens; the squamous portion in some specimens is as depicted by Coutière, arising abruptly at slightly more than half of the length of the outer spine, but in others it tapers gradually to near the tip of the spine, with most of the specimens intermediate in condition; in most the squamous portion is without setae as described by Coutière, but in a few there are some short feeble bristles along its margin; finally, the antennal peduncle varies from reaching the tip of the second antennular article to reaching only two-thirds its length. The large chela does not exhibit any marked variation. In the small chela most of the specimens have fingers more nearly 1.3 times the length of the palm than 1.0 as in the type specimen. Coutière remarked that the second leg varies from 2.2 to 4 times the length of the carapace; in a few of these specimens the second legs are almost 5 times the length of the carapace. On the third leg the spine on the inferior distal margin of the merus usually is small and subacute like that depicted by Coutière, but in several it is strong and acute, and in one it is reduced to a rounded protuberance; on the propodus there are usually seven instead of five spines. The telson usually approaches the proportions given by Coutière, but in some the tip is relatively broader so the length is only 3.2 times the breadth of the tip instead of 4.5. These variations do not appear to be consistent enough to be of taxonomic importance.

Alpheus perplexus sp. nov.

Fig. 13

(?) *Alpheus* species, de Man, Siboga Exped. 39a¹ (2): 349, pl. 15, fig. 71, 1911.

TYPES: Holotype, an 18.8 mm. male col-

lected by Preston E. Cloud, Jr., from locality A-7; allotype, an ovigerous female 20.4 mm. long, same location. Types to be deposited in the U. S. National Museum.

DESCRIPTION: Front of carapace straight (in type) to concave (in allotype); orbital hoods somewhat inflated and rounded; interorbital carina slight and rounded, not reaching to anterior margin of carapace or posterior to end of orbital hoods.

Second antennular article 2.1 times as long as visible portion of first, 2.3 times as long as third, and 3.3 times as long as broad. Stylocerite rounded. Scaphocerite reaching slightly beyond end of second antennular article; carpocerite reaching almost to end of third antennular article; basicerite unarmed.

Large chela of type specimen heavy, 2.8 times as long as broad, flattened, and with fingers occupying 0.2 of entire length. Only distal third of chela sculptured; superior crest interrupted by deep, abrupt transverse groove, distal to transverse groove crest thin, high, terminating in a rounded shoulder. Plaque crest heavy, rounded, separated from superior and inferior crest by deep grooves. Inferior crest pronounced, distally high and thin, terminating in a rounded shoulder flanking dactylus. Inferior shoulder rounded. Fixed finger very short, distally notched to receive dactylus. Dactylus closing almost across end of palm, heavy, rounded, nearly hammer-shape. Merus 0.3 as long as chela, 3.1 times as long as broad, without teeth or spines, with inferior external margin rounded.

Large chela of female of similar armature, but relatively much smaller than that of male, 3.9 times as long as broad.

Small chela lacking in male; in female chela 4.5 times as long as broad, with heavy fingers occupying distal 0.3; small tooth projects superior to articulation at approximately 90°.

Second legs long, strong, with merus about 0.7 as long as large chela in type. Carpal articles with ratio: 10:11:3:4:5.

Third legs with ischium armed with rather weak spine; merus almost 4 times as long as

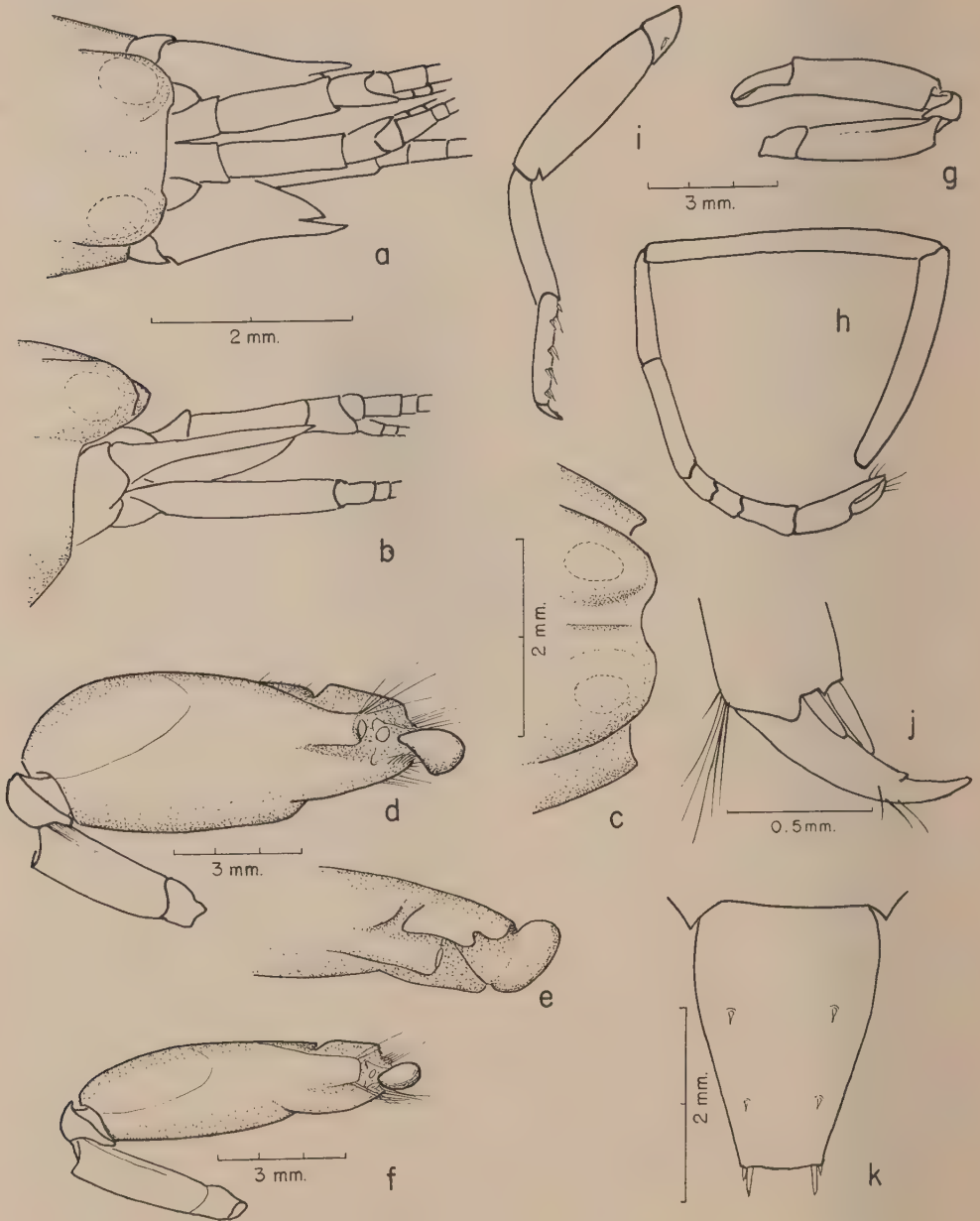


FIG. 13. *Alpheus perplexus* sp. nov. *a*, *b*, Anterior region, dorsal and lateral aspects, type specimen; *c*, anterior region, dorsal aspect, allotype (specimen asymmetrical); *d*, *e*, large cheliped, lateral and superior aspects, type specimen; *f*, large cheliped, allotype; *g*, small cheliped, allotype; *h*, second leg; *i*, third leg; *j*, third leg, dactylus; *k*, telson.

broad, armed with weak sub-acute tooth distally; carpus 0.7 as long as merus, unarmed except for two rounded projections distally; propodus 0.6 as long as merus, armed with one single and five pairs of spines on inferior margin; dactylus curved, with very slight secondary tooth. (on female secondary tooth somewhat larger).

Telson 3.3 times as long as posterior margin is broad, 2.3 times as wide anteriorly as posteriorly; sides slightly rounded, both pairs of dorsal spinules small, anterior pair 0.4, posterior pair 0.7 length of telson posterior to articulation. Inner uropod with several weak spinules on outer distal margin.

DISCUSSION: This species is difficult to assign to an infrageneric group, for the anterior carapace and second legs are very much like those found in the *Obesomanus* group, but the large chela is more like those found in the *Macrochirus* group. The dactylus of the large chela, which should be hammer-shaped in the *Obesomanus* group, is intermediate between the form found in many species of the *Megacheles* and *Macrochirus* groups and those found in the *Obesomanus* group.

Only on the basis of the lack of a rostrum and of orbital teeth was this species assigned to this group. Within the group it is definitely separated from all other named species by the form of the large chela and by the fact that the dactyli of the third and fourth legs carry a small secondary unguis.

The species appears to be similar to the specimen that de Man briefly described but left unnamed because it lacked both of the chelae and the second legs. Between the two specimens there are differences in proportions of the antennules, antennae, third legs and telson, but these differences are slight and probably not significant. Also de Man's specimen had a slight rostrum with the interorbital carina reaching to its tip, while neither of these specimens show a trace of the rostrum, and the interorbital carina terminates posteriorly to the margin of the carapace. This too, in view of the fact that the two specimens available

show some variation, and that marked variation has been reported for species showing a similar frontal region, may be without significance. The armature and general form of the 3rd legs are similar. (De Man described the stylocerite as acute, but figured it as similar to those of these specimens.)

The difference between the form of the large chela in the male and the female is interesting. While in most species the chela of the female is considerably smaller than that of the male, it is seldom that the proportions are so pronouncedly different. It is possible, of course, that these specimens represent two species, but as they are similar in other characteristics, as they bear similar sculpturing on the large chela, and as they were collected together at the same station, it seems unlikely that they are other than a single dimorphic species.

Alpheus chamorro sp. nov.

Fig. 14

TYPE: Holotype, a 7.5 mm. male collected by A. H. Banner. Specimen to be deposited in U. S. National Museum.

DESCRIPTION: Anterior margin of carapace projecting beyond orbital hoods as narrow, somewhat flattened shelf; rostrum small, tip rounded; rostral carina low but sharp, extending from behind orbital hoods to tip of rostrum. Orbital hoods inflated, rounded, and anteriorly set off by medial flat orbitocarinal area.

Second antennular article 1.7 times as long as broad; first and third articles subequal in length and 0.7 as long as second article; stylocerite short, anteriorly acute. Basicerite unarmed. Scaphocerite with heavy lateral spine reaching to end of third antennular article, with reduced squamous portion reaching to end of second article. Carpocerite longer than antennular peduncle.

Large chela round, inflated, 2.6 times as long as broad and 2.2 times as long as high (*i.e.*, when the dactylus is seen in profile), fingers occupying the distal 0.25. In profile,

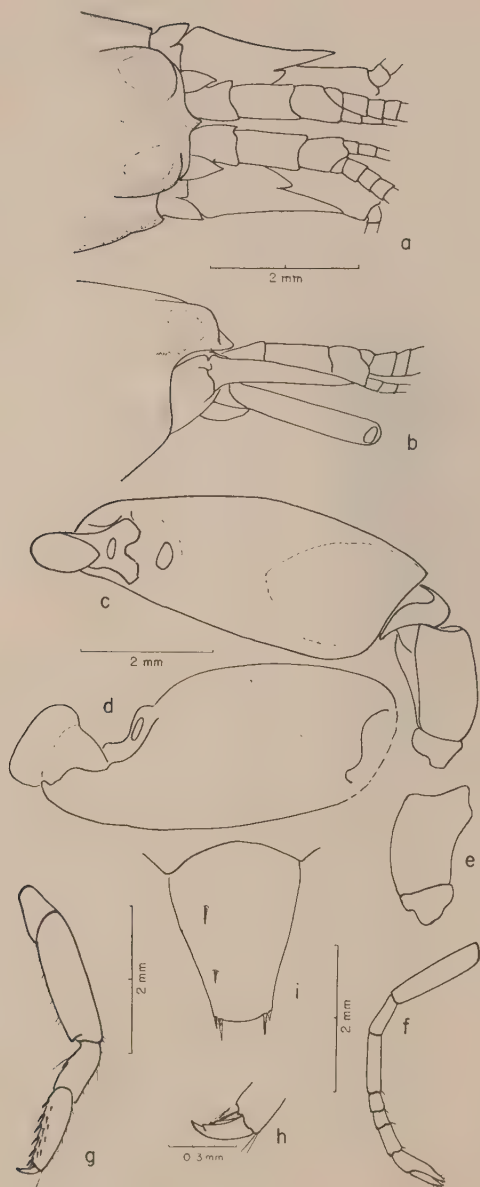


FIG. 14. *Alpheus chamorro* sp. nov. a, b, Anterior region, dorsal and lateral aspects; c, d, large cheliped, lateral and inferior aspects; e, merus, large cheliped, medial aspect; f, second leg; g, third leg; h, dactylus, third leg; i, telson (dorsal spinules lacking in specimen).

chela slopes abruptly toward articulation of dactylus; palmar adhesive plaque borne upon rounded eminence protruding from slope. Fixed finger short, cleft to accommodate dactylus. Dactylus short, heavy, but not as strongly hammer-shaped as in some other members of the group. Merus short, heavy, 0.4 as long as chela, outer face 1.4 times as long as broad; inferior internal margin bearing heavy rounded protuberance but otherwise unarmed.

Small chela lacking in specimen.

Carpal articles of second legs with ratio: 10:14.7:4.7:4.0:7.3.

Ischium of third legs unarmed. Merus 3.3 times as long as broad, bearing rounded tooth of moderate development on inferior distal margin. Carpus heavy, 1.6 times as long as broad, 0.35 as long as merus, armed with short heavy spine in middle of inferior margin and distally with two heavy subacute projections. Propodus correspondingly heavy, 0.6 as long as merus, armed with six pairs of spines along inferior and inferodistal margins, with scattered smaller spines adjacent. Dactylus strongly curved bearing small secondary unguis that is difficult to discern.

Uropods of usual form. Telson short, broad and abruptly tapering, 3.1 times as long as distal margin is broad, 2.3 times as wide proximally as distally; dorsal spinules well developed on left side only, anterior spinule 0.3, posterior 0.7 of length posterior to articulation.

DISCUSSION: While the general form, even to the shape of the anterior carapace and the secondary unguis on the dactylus of the third legs is very reminiscent of *A. paralcione* (Coutière) of the *Crinitus* subgroup, the hammer-shaped dactylus of the chela of this species shows that it definitely belongs to the *Obesomanus* subgroup.

Unlike all species of the *Obesomanus* subgroup except *A. perplexus* Banner (above) and, if distinct, *A. species de Man* (1911: 349), *A. chamorro* has a biunguiculate dactylus on the third legs.

This species can be distinguished easily from *A. perplexus* by the form of the large chela, which is rounded in this species but bears deep sculpturing in *A. perplexus*.

The comparison of this species, *A. perplexus* and de Man's *A.* species shows the difficulty of trying to identify an incomplete specimen, for although the chelae show that *chamorro* and *perplexus* are not even closely related, each is similar enough to de Man's description of his broken specimen to be confused with it. *A. chamorro* is quite like de Man's specimen in the configuration of the anterior carapace and the bases of the antennae and antennules, but dissimilar in the structure of the third legs; *A. perplexus* is less like de Man's specimen in the anterior carapace but more similar in the third legs. After careful consideration it appears that the legs are more constant in their character than the anterior carapace, so de Man's specimen has been assigned, but still with doubts, to *A. perplexus*.

It should also be noted that *A. chamorro* shows affinity to *A. bradypus* Coutière (1906: 891) in the *Crinitus* group. While there are

specific characteristics adequate to separate them easily, such as the dactylus of the third legs and the slight proximal projection of the "head" of the dactylus of the large chela, in general configuration the two species are strikingly similar, even to the shape of the eminence that bears the palmar adhesive plaque and the rounded protuberance on the inferior internal margin of the large chela. While the two species may merely show convergent evolution, or may be closely related on the limits of their respective groups, this may also indicate that the groups were separated upon artificial criteria.

The specific name has reference to the Chamorro people, the original inhabitants of the Mariana Islands.

Alpheus species 2

Fig. 15

SPECIMEN: A 11.2 mm. female, nonovigerous, collected by A. H. Banner.

DESCRIPTION: Anterior carapace without trace of rostrum, rostral carina, or orbito-rostral furrows but uniformly inflated and rounded over eyes.

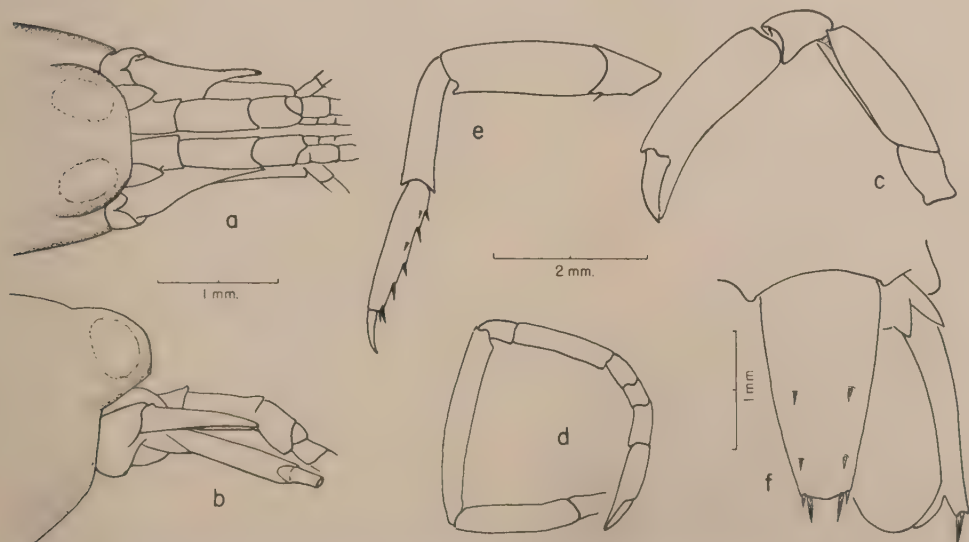


FIG. 15. *Alpheus* species 2. a, b, Anterior region, dorsal and lateral aspects; c, small cheliped; d, second leg; e, third leg; f, telson and uropods.

Antennular peduncle with second article 2.5 times as long as broad, 1.7 times as long as visible portion of first and third article which are subequal. Stylocerite without lateral spine, rounded, reaching half length of basal article. Upper flagellum slightly shorter than peduncle, lower shorter than upper. Basicerite unarmed. Lateral spine of scaphocerite reaching to end of second antennular article; flattened portion reduced, narrow, reaching only to first third of second antennular article. Carpocerite approximately as long as antennular peduncle. Flagellum of usual form.

Large chela lacking. Small chela rounded, regular, slightly curved toward fingers, 4.0 times as long as broad, with fingers occupying distal 0.3. Carpus somewhat elongate. Merus unarmed, outer face 3.6 times as long as broad, 0.7 as long as chela.

Carpal articles of second legs with ratio: 10:30:8:7:13.

Ischium of third legs bearing reduced spine. Merus 4.1 times as long as broad, distal inferior margin bearing tooth of moderate size. Carpus 0.66 as long as merus, distally produced into superior and inferior acute teeth of moderate size. Propodus 0.83 as long as merus, bearing eight spines irregularly placed on inferior and distal margins. Dactylus simple, curved, 0.26 as long as merus.

Telson 2.8 times as long as posterior margin is wide; anteriorly 1.5 times as wide as posteriorly; margins very slightly convex. Uropods of normal form; distal spine of outer uropod not black.

DISCUSSION: Without the large chela on this specimen, it is impossible to assign it even to group. The reduction of the orbital teeth and the reduction of the scaphocerite together with the armature of the third legs, would indicate that it may belong to the *Obesomanus* group, but, without knowing whether the dactylus of the large chela is hammer-shaped or not, it cannot be assigned for certain. Certainly the unique character of the front of the carapace does not show close

relationship to any group or to any species of the genus *Alpheus* known to me.

The form of the rostral front appears to be similar to that described by Armstrong (1949: 12) as characteristic of his new genus, *Thunor*. However, on all other characteristics for this genus—absence of the cardiac notch on the carapace, the absence of anal tubercles, the absence of an articulation in the outer uropods (the ocular beak was not examined)—this species differs from *Thunor* and resembles *Alpheus*. In view of the wide variation in the rostral front found in *Alpheus* the one similarity was not considered to be of generic importance.

Because the specimen is imperfect it has been left unnamed.

Crinitus subgroup

Alpheus claudi sp. nov.

Fig. 16

TYPE: Holotype, a unique ovigerous female 17.6 mm. long, collected by Preston E. Cloud, Jr., at locality D-5. Specimen to be deposited in the U. S. National Museum.

DESCRIPTION: Body form short, heavy. Anterior portion of carapace depressed when seen in lateral view. Orbital hoods inflated, rounded, demarked from anteromedial portion of carapace and overhanging anterolateral portion. Anteromedial portion of carapace broad, flat, projecting, margins almost straight; rostrum proper poorly demarked from adjacent portions of carapace, short, broad, with tip reaching beyond middle of visible portion of first antennular article. Rostral carina low but sharp reaching posteriorly from tip of rostrum to slightly behind orbital hoods. Eyes small, not filling orbital hoods.

Second antennular article about 2 times as long as broad, 1.3 times as long as visible portion of basal article, 2.4 times as long as distal article. Stylocerite short, heavy, with acute tip reaching almost to end of first antennular article. Basicerite bearing small spine. Scaphocerite reaching to near end of

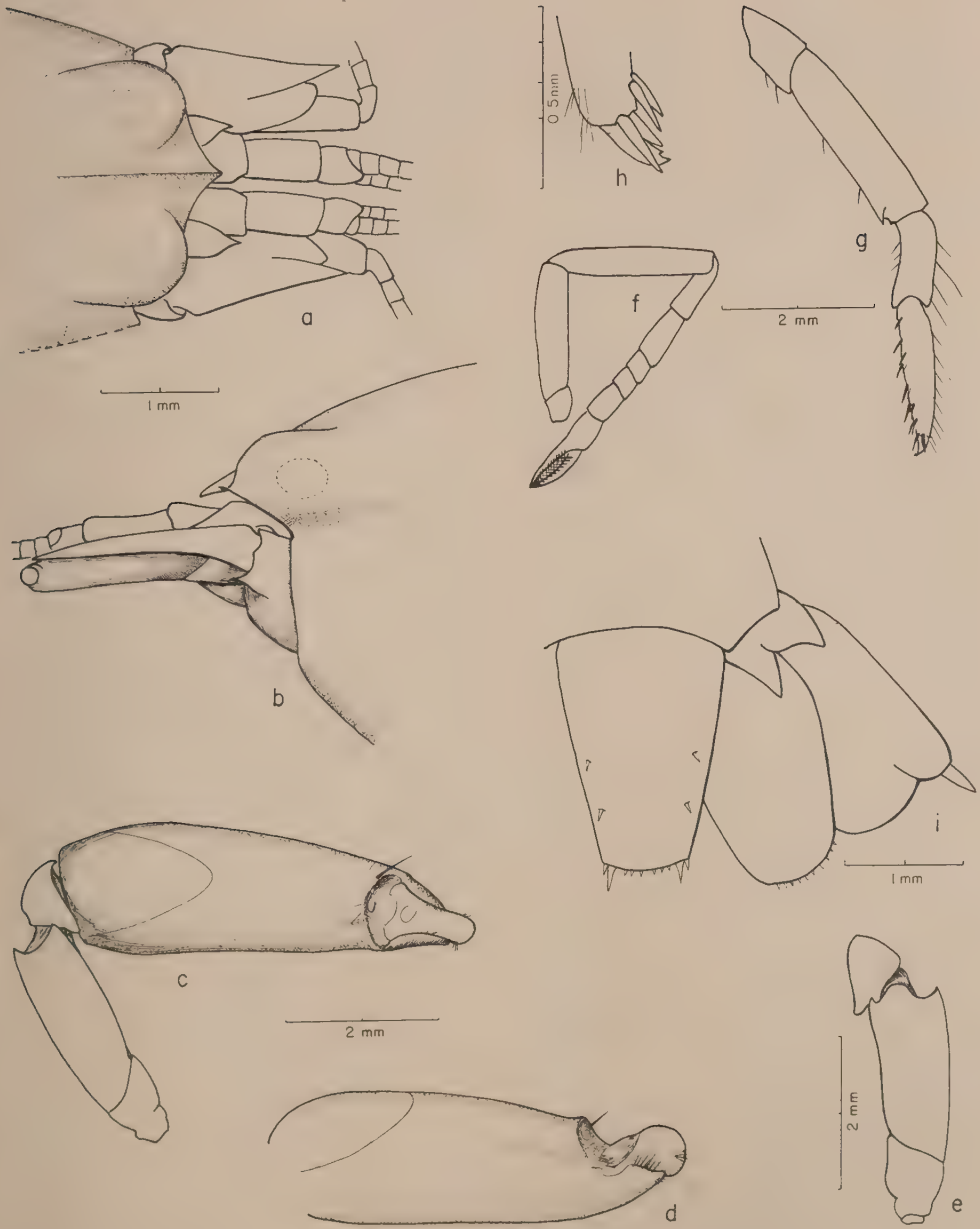


FIG. 16. *Alpheus claudi* sp. nov. a, Anterior region, dorsal aspect (right margin distorted in specimen but reconstructed in drawing); b, same, lateral aspect; c, large cheliped, lateral aspect; d, large chela, inferior aspect; e, large cheliped, merus, medial aspect; f, second leg; g, third leg; h, third leg, dactylus, posterior or lateral aspect; i, telson and uropod.

antennular peduncle, squamous portion reaching to end of second antennular article; outer margin almost straight. Carpocerite reaching slightly beyond end of antennular peduncle and scaphocerite.

Large chela subcylindrical, as broad as high, slightly tapering distally, 3.1 times as long as broad. Palm below and immediately proximal to adhesive plaque with slight longitudinal depression. Dactylus 0.23 as long as entire chela, somewhat crested, rounded. Chela almost devoid of setae. Merus 2.6 times as long as broad, almost 0.5 as long as chela; superior margin distally projecting as small rounded tooth; inferior internal margin terminating distally in small acute tooth that is difficult to discern.

Small chela lacking.

Second legs relatively short, heavy. Carpal articles with ratio: 10:9:3.5:3.5:5.5; first article 3 times as long as broad. Chela 1.5 times as long as first carpal article, palm occupying slightly over 0.3 the entire length; fingers arched, tips crossing, bearing stiff combs of setae that cross.

Third legs heavy, ischium unarmed. Merus 4 times as long as broad, distal inferior margin armed with tooth of moderate development.

Carpus 0.38 as long as merus, both distal margins projecting as rounded teeth. Propodus 0.7 as long as merus, strongly tapering, distally only half as broad as proximally; inferior margin bearing 11 strong acute spines. Dactylus short, partially hidden, especially in anterior or median view, by propodal spines, some of which are equal in length to dactylus; dactylus heavy, curved, bearing slight biunguiculation that is difficult to discern both because of spines and normal rotation of dactylus.

Abdomen broad, rather soft. Sixth abdominal segment without spines or teeth. Telson 2.0 times as broad anteriorly as posteriorly, 3.4 times as long as broad posteriorly; sides straight, posterior margin slightly arcuate; anterior pair of dorsal spinules 0.5, posterior pair 0.8 of distance to tip from articulation;

tip bearing about six very small spinules in addition to usual posterolateral spines. Uropods of usual form, inner bearing about 10 spinules along distolateral margin similar to those on tip of telson.

DISCUSSION: This species apparently belongs to the *Crinitus* subgroup in spite of the fact that the chela bears a short, shallow, longitudinal groove. Within the group it appears to be most closely related to the species *A. alcyone* de Man, *A. providencei* Coutière, *A. arethusa* de Man, and *A. paralcione* Coutière. From *A. alcyone* it may be separated by the lack of spines on the merus of the third legs as well as other characteristics. It is separated from *A. arethusa* and *A. paralcione* by a combination of characters, one of the more conspicuous being the lack of spines or teeth on the sixth abdominal segment. It appears to be somewhat related to *A. providencei*, especially in the frontal regions of the carapace, the antennular and antennal peduncles, the general form of the third leg and the trace of biunguiculation of its dactylus but it can easily be separated by the more elongate rostral triangle, the presence of a spine on the basicerite, the more elongate large chela, the armature of the merus of the cheliped, the shorter second article of the carpus of the second legs, the short dactylus of the third legs, and the form and armature of the uropods and telson.

The species was named in honor of Preston E. Cloud, Jr., U. S. Geological Survey, who collected this and many of the other specimens reported in this study.

Alpheus brevipes Stimpson

Alpheus brevipes Stimpson, Acad. Nat. Sci. Phila., Proc. 12: 30, 1860.

Crangon brevipes (Stimpson) Banner, Pacific Sci. 7(1): 103, figs. 35-37, 1953. [Neotype established.]

LOCALITIES: Banner, 2 specimens in 2 collections; Cloud, 8 specimens at Loc. D-8, 1 at Loc. 6.

DISCUSSION: These specimens, together

with the specimens from Arno, Onotoa, and Palmyra to be reported upon in later papers, parallel the variation already reported from Hawaii (Banner, 1953: 103). It should be noted under the variation of the frontal region of the carapace that only rarely were the "Orbital hoods acute in front, with their apices curved inward," a characteristic given by de Man in his key (1911: 315); instead the ridges of the orbital hoods were usually rounded, and often did not slope medially towards the ventral side.

Alpheus bucephalus Coutière

Alpheus bucephalus Coutière, Fauna and Geog. Mald. and Laccad. 2: 890, pl. 78, fig. 29, 1905.

LOCALITIES: Banner, 12 specimens in four collections; Cloud, 3 specimens at D-5, 3 at D-8, 1 at E-4, 1 at FX.

DISCUSSION: Several of the larger male specimens which otherwise agree with the characteristics of the species have broadened fingers on the small chelae, a trait that is not supposed to occur in this species. However, as the specimens are similar to *A. bucephalus* in all other characteristics, and as they were in a mixed collection with smaller specimens without the broadened finger, they have been assigned to this species. This peculiarity will be discussed in a future paper.

Alpheus bradypus Coutière

Fig. 17

Alpheus bradypus Coutière, Fauna and Geog. Mald. and Laccad. 2: 891, pl. 78, 79, fig. 30, 1905.

LOCALITY: Banner, 8 specimens in 1 collection, Saipan.

DISCUSSION: This group of eight specimens agree quite well with Coutière's description of his two damaged specimens. The most conspicuous differences between the two lie in the following characteristics: 1, The second antennular article is slightly longer than that

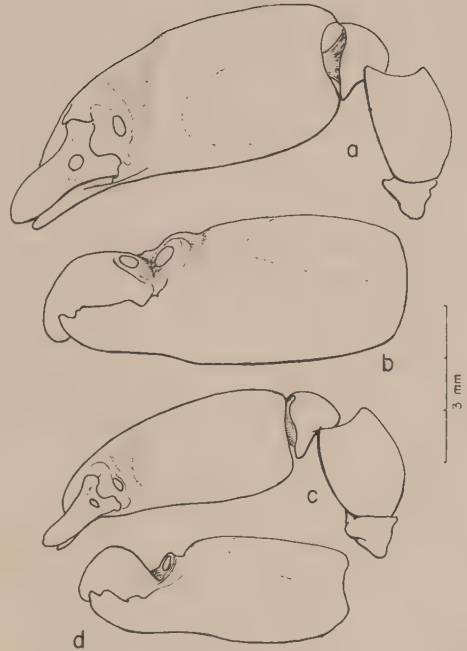


FIG. 17. *Alpheus bradypus* Coutière. a, b, large chela male; c, d, large chela, female.

described by Coutière. 2, There is a small, poorly developed and difficult to discern tooth on the basiscrite, while Coutière reported his specimens as unarmed. 3, In none of the males did the dactylus of the small chela show the fringe of setae depicted by Coutière; moreover the small chelae of the males and females were more alike, showing less sexual dimorphism. 4, The internal ramus of the uropods bears a row of numerous, although poorly developed denticles along its distal margin. These differences may in part be due to individual variation, so common in related species of this group, or they may be due to geographical variation; certainly it seems inadvisable at the present state of knowledge of the species to divide it into subspecies on the basis of these characteristics.

Both of Coutière's specimens were without the large chela. As most of these specimens are complete, I have shown the chelae of a mature male and a mature female in Figure

17. These chelae are dimorphic both in size and proportions. However, in both sexes there is a poorly demarked shallow depressed area on the upper side of the chela proximal to the articulation of the finger. This depression appears slightly more distinct in the female than in the male, possibly because the chela is more slender. The merus is unarmed on all margins but the inferior internal margin projects slightly distally.

There is some variation in the proportions of the antennular peduncle. The scaphocerite in one specimen, instead of reaching slightly past the middle of the third antennular article, reaches beyond it by half its length. In the same specimen the reduced squamous portion of the scaphocerite gradually tapers to its end which is opposite the distal end of the second antennular article instead of being more abruptly truncate opposite to the middle of the same article. Otherwise this specimen is similar to the others.

Alpheus eulimene de Man

Alpheus eulimene de Man, Siboga Exped. 39a¹
(2): 364; pl. 16, fig. 76, 1911.

LOCALITY: Cloud, 2 specimens at C-7a, 10 April 1949.

DISCUSSION: *A. eulimene* de Man and *A. styliceps* Coutière (1905: 889, pl. 78, fig. 28) are very closely related species, separated principally by the form of the frontal portion of the carapace and by the proportions of the third leg and the armature of the fourth. The two specimens from Saipan, a 9.0 mm. female and a broken and distorted male of 7.8 mm., lie somewhat intermediate between the two species. In *A. eulimene* the front of the carapace is almost straight in front of the orbital hoods, abruptly giving rise in the middle to a very short rostrum; it bears a dorsal carina that continues posteriorly to the middle of the carapace. In *A. styliceps* the anterior margin of the carapace curves gradually into a larger rostrum, but the carina does not extend posteriorly to the orbital hoods. In these spec-

imens the rostrum is like *A. styliceps*, except that the curve is less gradual and the base of the rostrum more abrupt; the dorsal carina is like *A. eulimene*. In *A. eulimene* and in these specimens the merus of the third legs is slightly over 4 times as long as broad, while in *A. styliceps* it is only 3 times as long; in de Man's species and in these specimens the merus of the fourth leg is unarmed, while in Coutière's it bears a strong distal tooth. If the distinction between these species is maintained after more specimens are examined, then these two specimens appear to belong to de Man's species.

There are several further minor differences between these specimens and de Man's description. In the male the scaphocerites are asymmetrically developed, with that of the right being reduced as described by de Man, but that of the left better developed, with the tip of the lateral spine reaching beyond the end of the antennular peduncle and the squamous portion reaching to the middle of the third, not the second, antennular article. In the female the palm of the small chela is 1.9 times as long as broad and as long as the fingers, instead of 1.5 times as long as broad and longer than the fingers. Unfortunately the small chela is lacking in the male. De Man gives lengths for the articles of the carpus of the second leg which produce the ratio of 10:14.4 for the first two articles, yet his drawing shows a ratio of 10:17.5, more like these specimens (in the female they have the ratio of 10:18.5). Finally, in the dactylus of the third leg, de Man shows a uniform tapering curve, but these specimens have a rounded thickening two-thirds of the length distally, similar to that described for *A. gracilis* var. *simplex* (Banner, 1953: fig. 25k).

Alpheus pachychirus Stimpson

Alpheus pachychirus Stimpson, Acad. Nat. Sci. Phila., Proc. 12: 30, 1860.

LOCALITIES: Banner, 1 specimen; Cloud, 1 specimen at E-4, 3 at Loc. 9.

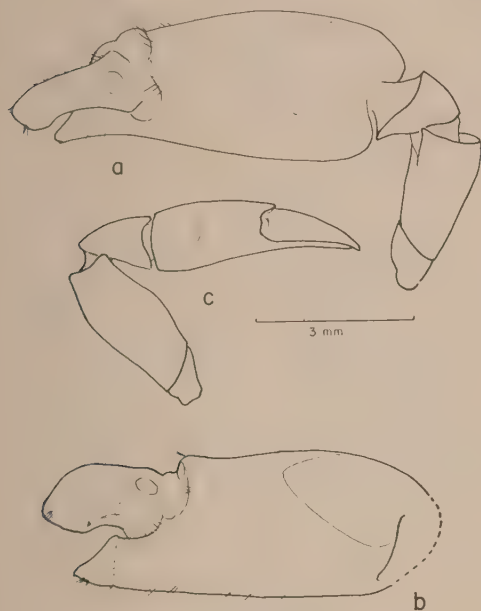


FIG. 18. *Alpheus ovaliceps* Coutière. *a*, *b*, Large chela; *c*, small chela.

Alpheus ovaliceps Coutière

Fig. 18

Alpheus ovaliceps Coutière, Fauna and Geog. Mald. and Laccad. 2(4): 888, pl. 77, fig. 27, 1905.

LOCALITY: Banner, 3 specimens, Saipan.

DISCUSSION: This species was described by Coutière on the basis of a single male from Minikoi. It has not been reported since then.

These three specimens, two males and a female, agree almost perfectly with the description and figures of Coutière, even to the two long and broadened bristles on the penultimate article of the third maxilliped. However, they do differ in two characteristics. In the Indian Ocean specimen the large chela had a marked taper towards the dactylar articulation and proximal to this articulation there was a slight transverse groove; in the present specimen, the chela maintains its full diameter throughout, and there is no such groove. The small chela is essentially similar

in the two sets of specimens. (I have drawn the small cheliped of the female particularly to show the form of the merus, similar in both sexes.) Secondly, the outer spine of the uropod was reported by Coutière as being dark brown, whereas in these three specimens it is colorless.

Within this group variations are so common that no great significance is attached to these differences. Possibly if other specimens from the Indian Ocean are compared to these from the Western Pacific the differences would be found to intergrade; if they did not, at most they would justify the erection of a subspecies for the Pacific form.

Alpheus frontalis Milne-Edwards

Alpheus frontalis Milne-Edwards, Histoire Naturelle des Crustacés, 2: 356, 1837.

LOCALITY: Banner, 1 specimen, Saipan.

Diadema subgroup

Alpheus diadema Dana

Alpheus diadema Dana, U. S. Explor. Exped. 13: 555, pl. 35, fig. 7, 1852.

Alpheus insignis Heller, K. Akad. Wiss. Wien, Sitzungber. 44: 269, taf. 3, fig. 17–18, 1861.

Crangon diadema Banner, Pacific Sci. 7(1): 118, fig. 43, 1953. [Neotype established.]

LOCALITIES: Banner, 15 specimens in 3 collections; Cloud, 18 specimens at locality D-5, 1 at Loc. 8.

Alpheus gracilipes Stimpson

Alpheus gracilipes Stimpson, Acad. Nat. Sci. Phila., Proc. 12: 31, 1860.

Crangon gracilipes Banner, Pacific Sci. 7(1): 115, fig. 41, 1953.

LOCALITIES: Banner, 55 specimens from 8 collections; Cloud, 10 specimens at locality D-5, 2 at D-6.

DISCUSSION: The specimens of this species from Hawaii bear balaeniceps-shaped dactyli on the small chelae in both sexes; in these from Saipan, however, only the small chela

of the males is broadened and bears the characteristic fringe of setae. In the females the dactylus is slender, tapering uniformly to the acute tip, and lacking all traces of the fringe. Both sexes lack the slight transverse depression proximal to the dactylus.

It is likely that this is a separate subspecies, distinct from the form in Hawaii. However, the decision will be deferred until specimens are examined from other archipelagoes. When Tahitian specimens (the type locality) are examined it will be possible to decide, if a new name is to be applied, which form is similar to Stimpson's type.

***Alpheus paracrinatus* Meirs var.
bengalensis Coutière**

Alpheus paracrinatus var. *bengalensis* Coutière,
Fauna and Geog. Mald. and Laccad. 2(4):
901, pl. 82, figs. 37-37a, 1905.

LOCALITIES: Banner, 17 specimens in 7 collections; Cloud, 1 specimen each at localities A-5, D-5, FX.

DISCUSSION: Variation is found in these specimens in the relative lengths of the antennular peduncle, the scaphocerite, and the carpocerite. In most the antennular peduncle does not reach to the tips of the other two, and most often the scaphocerite and the carpocerite are subequal. Only on a few specimens is the carpocerite considerably longer than the scaphocerite, as was commonly found in Hawaii (Banner, 1953: fig. 40a, b). In some specimens, on the other hand, the tips of the three parts reach essentially the same point. Variation is also found, as in Hawaii, in the armature of the merus of the large and small chela. In several specimens the fingers of the large chela are proportionately shorter, not more than about 0.2 the length of the chela; in other specimens the fingers of the small chela are much more hirsute. In all of the specimens the first and second articles of the second leg are subequal, the criterion for the separation of this variety from the parent species.

Brevirostris group

***Alpheus rapax* Fabricius**

Alpheus rapax Fabricius, Sup. Ent. Syst., p. 405, 1798 [see de Man, 1909: 147-155 for synonymy].

LOCALITY: Guam, collected by Seale, 1900 (Bernice P. Bishop Mus. No. 161).

DISCUSSION: This sole specimen is definitely *A. rapax* as redescribed by de Man. The Hawaiian specimen of this species showed two differences from de Man's redescription: the merus of the small cheliped was lacking in a distal spine on the inferior internal margin, and the third legs were not densely hirsute. This specimen has a very small tooth on the merus, but, as in the Hawaiian specimen, the third legs bear only scattered setae.

***Alpheus* species 3**

Fig. 19

LOCALITY: A 12 mm. male from Loc. 2, collected by P. E. Cloud, Jr.

DESCRIPTION: Rostrum acute, reaching about 0.7 length of visible portion of first antennular article, rostral triangle slightly longer than broad. Rostral carina strong, extending posteriorly half length of carapace. Orbital hoods inflated, rounded, similar in development to *A. rapax* Fab.

Second antennular article twice as long as broad, 1.3 times as long as first article, about 2 times as long as third. Stylocerite with acute lateral tooth projecting almost to end of first antennular article. Spine of basicerite of moderate development, relatively shorter than stylocerite. Scaphocerite with tip of lateral spine noticeably longer than antennular peduncle; spine exceeding flattened portion in length. Carpocerite slightly longer than scaphocerite.

Third maxillipeds, if extended straight, reaching beyond antennular peduncle. Last article 3.0 times as long as penultimate and 4.0 times as long as broad.

Merus of large cheliped 2.8 times as long

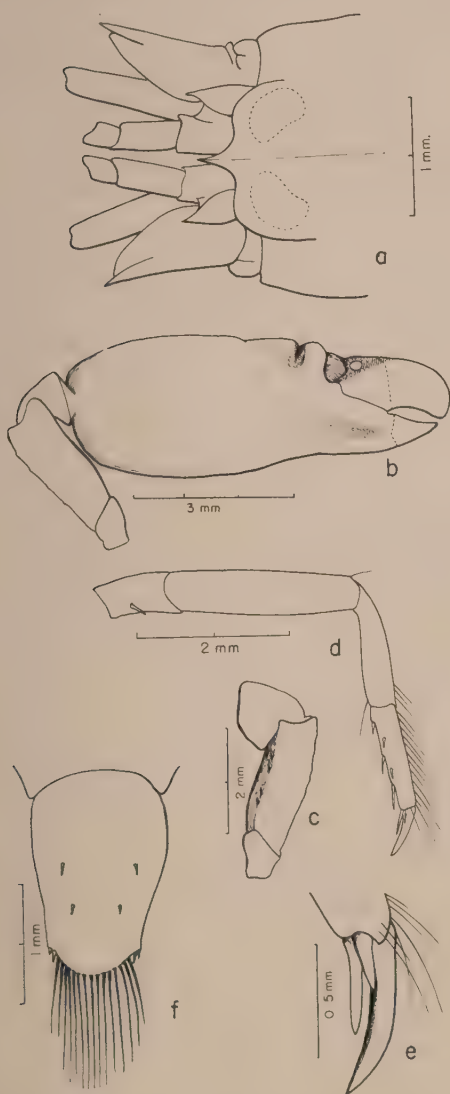


FIG. 19. *Alpheus* species 3. *a*, Anterior region, dorsal aspect; *b*, large chela; *c*, large cheliped, merus; *d*, third leg; *e*, third leg, dactylus; *f*, telson.

as broad, superior margin slightly irregular, inferior internal margin bearing four irregularly placed moveable spines. Chela 2.5 times as long as broad, with palm 1.85 times as long as fingers, with short transverse groove on superior margin, shallow depression on

external face of base of fixed finger; chela with but few scattered setae.

Small cheliped and second legs lacking.

Ischium of third legs 0.3 as long as merus, bearing movable spine. Merus slightly over 4 times as long as broad, unarmed. Carpus half as long as merus, unarmed. Propodus tapering, as long as carpus, bearing five strong spines on or near inferior margin and two distally. Dactylus half as long as propodus, simple, curved, somewhat flattened on inferior margin. Distal end of carpus and entire propodus bearing long fine setae along superior margin.

Telson in specimen asymmetrical, 2.2 times as long as posterior margin is broad, anteriorly 1.4 times as broad as posteriorly; lateral margins anteriorly convex, posteriorly concave, with convexity of right side more pronounced than left; tip broadly arcuate. Dorsal and terminal spines of slight development.

DISCUSSION: It is unfortunate that this specimen is in such poor condition; in addition to lacking the small chela, both second legs, one of the third legs, both fourth legs and one of the fifth legs, the tissue within the exoskeleton is partially shrunken and withdrawn, leaving the exoskeleton without support; the exoskeleton, as a consequence, is difficult to discern and often distorted.

The form of the chela and the anterior carapace plainly places this species within the *Brevirostris* group. The groove of the chela, together with the keel on the carapace, the lack of a tooth on the merus of the third leg, and the narrowness of the same article serves to separate this species from all other species in the group except *A. brevirostris* (Olivier) and *A. savuensis* de Man. It is plainly different from the former in the scaphocerite, for in *A. brevirostris* the flattened portion reaches almost to the tip of the spine (de Man, 1909: fig. 15), and in the large chela, which appears much heavier in the palm and which has a dactylus that is about three times as heavy as the fixed finger (Coutière, 1899: fig. 281).

This form shows a closer relationship to *A. savuensis*, but can be separated from that species by a series of characteristics such as: the rostrum, which is shorter in *A. savuensis*; the rostral carina, which reaches only slightly past the orbital hoods; the stylocerite, which does not bear an acute tip like this form; slight (and possibly not significant) differences in the relative lengths of the antennular peduncle, scaphocerite and carpocerite; similar differences in the dactylus of the third legs, which de Man describes as not flattened, but which are slightly flattened on the inferior face in this specimen. In spite of these differences, which at best are minor, there appears to be much in common in general form between the two, especially in the large chela and third legs.

As the small chela and the second legs are so important in the separation of species in this genus and group, to say that this sole mutilated specimen is or is not the same as *A. savuensis* would be questionable. Likewise, if the specimen were considered as distinct from de Man's, little could be gained by the establishment of this defective specimen as a type for a new species.

Edwardsi group

Alpheus ladronis sp. nov.

Fig. 20

TYPES: Holotype, a 10.8 mm. male, collected by A. H. Banner, Saipan; allotype, a 13.0 mm. ovigerous female; paratype, a partially broken ovigerous female, same length; both females from same collection as male. Types to be deposited in the U. S. National Museum.

DESCRIPTION: Rostrum small, acute, reaching almost to middle of visible portion of first antennular article; lateral margins of base demarked from almost straight orbitorostral margins; sharp rostral carina extending to near posterior margin of eyes, continuing low and rounded, and soon merging with curvature of carapace; in lateral view carina higher

than orbital hoods, depressed anteriorly. Orbital hoods relatively low, rounded, separated from carina by shallow rounded depressions.

Second antennular article 1.7 times as long as broad, 1.1 times as long as first, 1.5 times as long as third. Stylocerite reaching to end of first antennular article. Basicerite armed with small, acute tooth. Lateral spine of scaphocerite reaching to end of third antennular article, squamous portion almost as long. Carpocerite reaching slightly beyond end of scaphocerite.

Large chela compressed, 2.6 times as long as high, with fingers occupying the distal 0.3. Transverse groove proximal to dactylar articulation shallow and rounded, continuous on inner face as shallow rounded depression, U-shaped in outline, and on outer face as deeper, well-delimited groove extending proximally past middle of palm. Shoulder on inferior margin conspicuous, extending up both inner and outer faces. Dactylus and fixed finger with acute tips. Merus 0.3 as long as chela, with outer inferior margin rounded, superior distal margin slightly produced into a low, obtuse tooth, inferior internal margin bearing a strong tooth subterminally.

Carpus of second legs with ratio: 10:7:3:3:6.

Small chela 4.1 times as long as broad, fingers slender, tapering (not belaeinceps-shaped), occupying distal 0.6. Merus slender, unarmed.

Third legs with ischium unarmed; merus 4.6 times as long as broad, carpus 0.5 as long as merus, with superior margin continuing distally as rounded projection; propodus 0.77 as long as merus, armed along inferior margin with six relatively long, slender spines; dactylus simple, curved, slightly less than 0.3 as long as merus.

Telson 2.1 times as long as broad posteriorly, 1.6 times as broad anteriorly as posteriorly; margins rounded, with arcuate posterior margin a continuation of curved lateral margins. Dorsal spinules on type asymmetrical, as shown in Figure 20*i*. Lateral spine

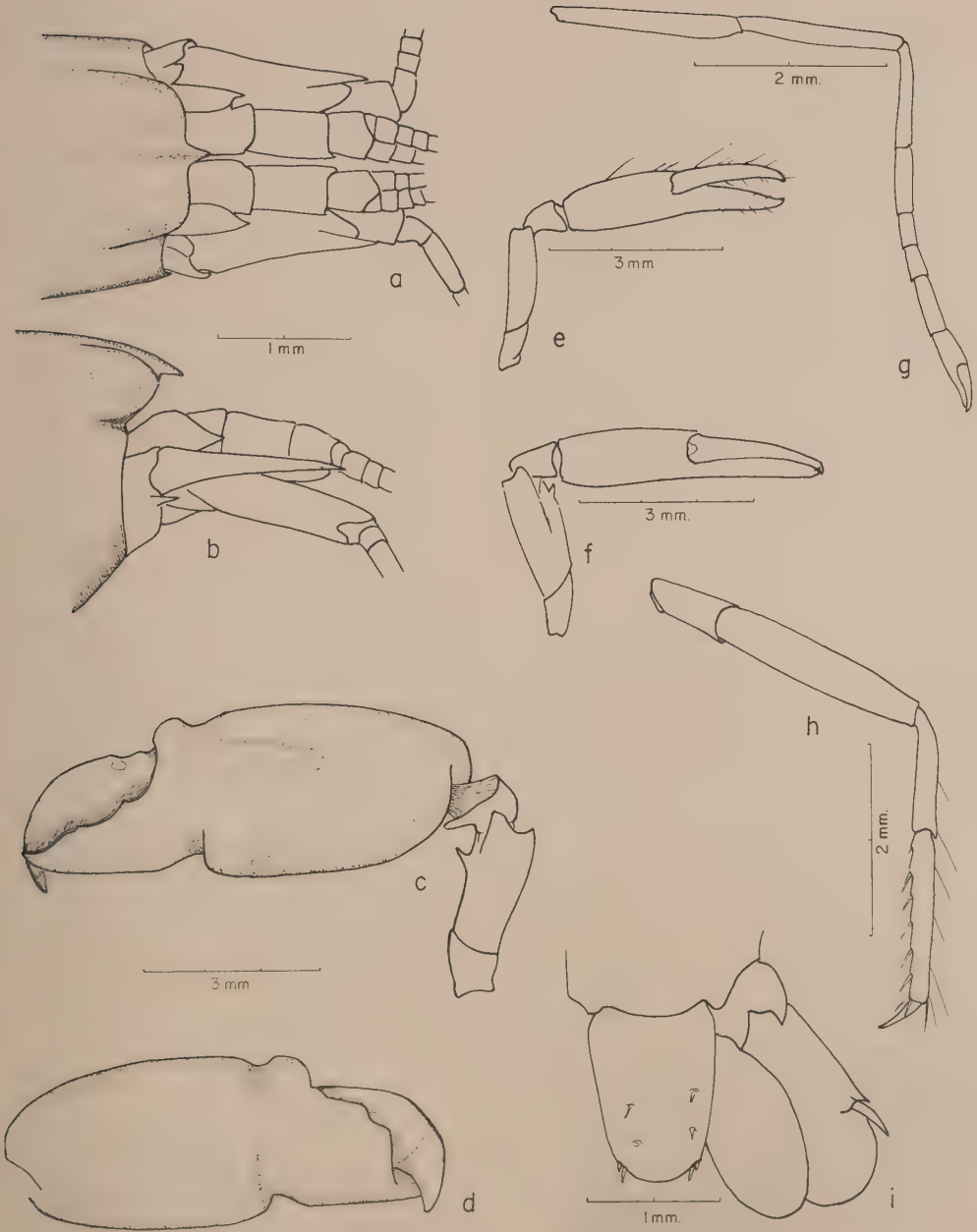


FIG. 20. *Alpheus ladronis* sp. nov. *a, b*, Anterior region, dorsal and lateral aspects; *c, d*, large chela, lateral and medial aspects; *e*, small cheliped, male (type); *f*, small cheliped, female (allotype—setae not shown); *g*, second leg; *h*, third leg; *i*, uropods and telson.

of outer uropod strong but exceeded by distal curved margin.

DISCUSSION: The two paratypes differ in two important ways from the type: in both the merus of the small chela carries a tooth similar to that of the large cheliped, and in both the margins of the telson are less rounded, with a more pronounced taper in the posterior half (in one the anterior margin is 1.9, in the other 3.0, times the breadth posteriorly). Other lesser differences were noted in the fingers of the large chela, which are more rounded, in slight difference in proportions in the carpus of the second legs, and in the uropods, which do not protrude as far beyond the lateral spine. It is likely that the difference in the fingers of the large chela, and it is possible that difference in the armature of the merus of the small chela, are secondary sexual characteristics; the other differences probably are normal variation.

This species plainly belongs to the Edward-sii group, and within that group appears to be most closely related to *A. bouvieri* A. Milne-Edwards and *A. bastardi* Coutière. From the latter it differs in the form of the rostrum, the more slender form of the small cheliped, and, if a specimen from Yap to be reported in a later publication is the same as Coutière's species, in the presence of the meral spines of the large chela and the absence of ischial spines of the third legs. From *A. bouvieri* it differs most notably in the absence of sexual dimorphism in the small chela; it apparently also differs in the presence of teeth on the basicerite and the merus of the large chela. Unfortunately, complete descriptions are not available for either of the species and it is possible that *ladronis* will be found either to be more closely related or more widely separated when the types are compared.

The specific name is derived from Magellan's name for the Mariana Islands.

Alpheus pacificus Dana

Alpheus pacificus Dana, U. S. Explor. Exped. 13: 544, pl. 34, fig. 5, 1852.

Crangon pacifica Banner, Pacific Sci. 7(1): 138, fig. 50. [Neotype established.]

LOCALITY: Banner, 2 specimens from one locality, Saipan.

DISCUSSION: Although these specimens are small and immature, they compare well to specimens of similar size from Hawaii. It is notable that in the large collection of specimens from Saipan only two specimens of this species were found, yet it is one of the most common in Hawaii.

Alpheus leptochirus Coutière

Alpheus leptochirus Coutière, Fauna and Geog. Mald. and Laccad. 2(4): 914-916, pl. 87, fig. 54, 1905.

SPECIMEN: Banner, a single specimen, Saipan.

DISCUSSION: This sole specimen, a male, is very similar to the female reported from Hawaii (Banner, 1953: 133, fig. 48) in all characteristics, and in those points where the Hawaiian specimen differs from the type, it is more similar to the Hawaiian specimen than to the type, except that in the first two carpal articles of the second leg the ratio is 10:9, intermediate between the ratio of 10:11 in the Hawaiian specimen and 10:7 in the type. Another slight point of difference is in the armature of the merus of the small and large chelae, which, instead of bearing movable spines as did the previous forms, bear short stiff setae.

Alpheus dolerus sp. nov.

Fig. 21

TYPES: Holotype, a 17.0 mm. male collected on Saipan in 1944 by A. H. Banner; allotype, a 14.6 ovigerous female from the same collection; paratypes, 12 specimens in 6 collections by A. H. Banner; 1 specimen from Loc. 6, collected by P. E. Cloud, Jr.

DESCRIPTION: Rostrum acute, reaching to end of first antennular article, continued posteriorly to slightly behind corneas as low

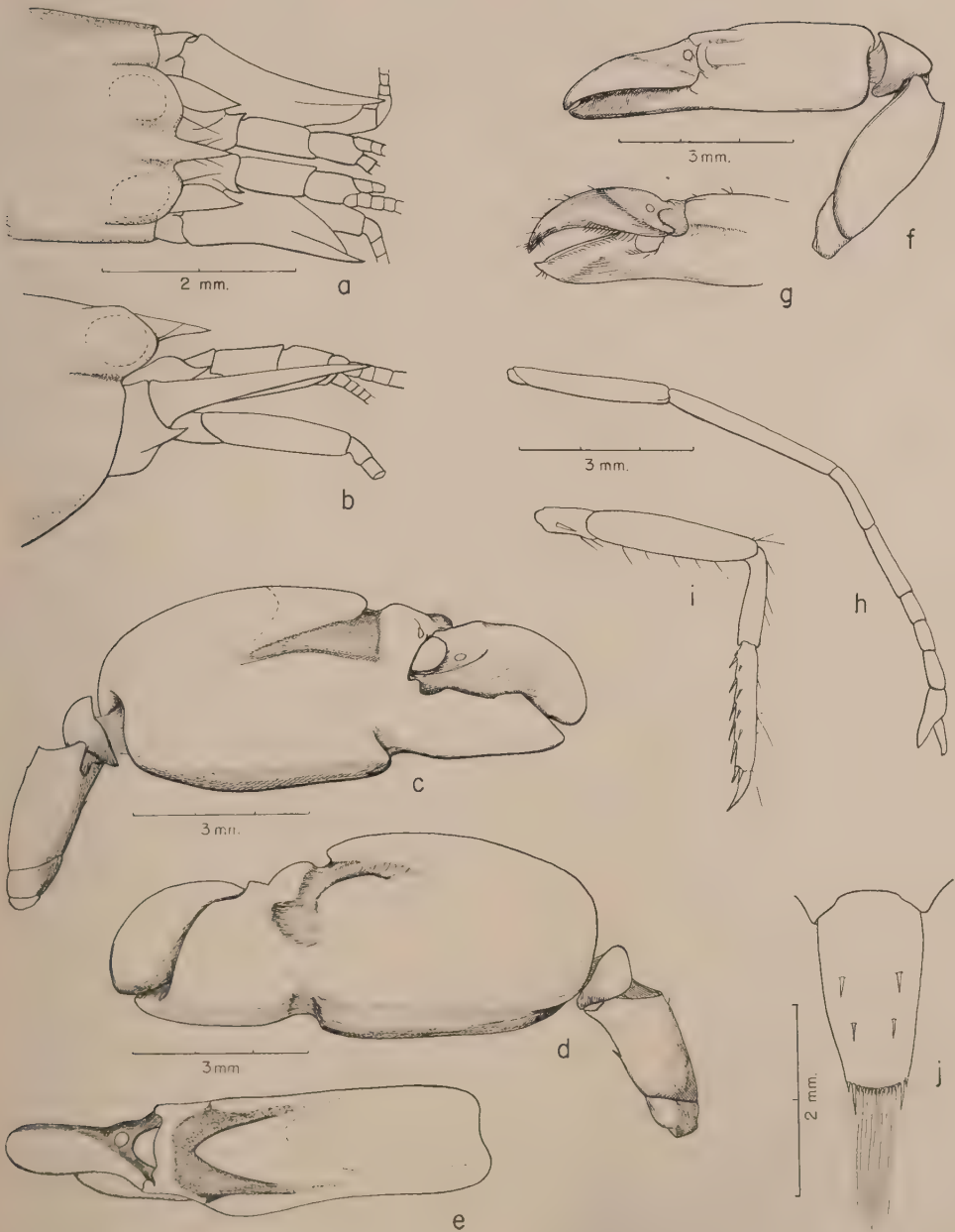


FIG. 21. *Alpheus dolerus* sp. nov. a, b, Anterior region, dorsal and lateral aspects; c, d, e, large chela, lateral, medial and dorsal aspects; f, g, small chela; h, second leg; i, fourth leg; j, telson.

rounded ridge; lateral margins bearing two stiff setae. Orbital hoods rounded, slightly inflated; orbitorostral area depressed, shallow, rounded.

Second antennular article twice as long as broad, slightly longer than first and third articles; lateral spine of stylocerite reaching to end of first antennular article. Lateral spine of basicerite small but acute; tip of spine of scaphocerite reaching beyond end of antennular peduncle; squamous portion of scaphocerite narrow, reaching to end of antennular peduncle; carpoperite slightly shorter than scaphocerite.

Large chela compressed, massive, 2.6 times as long as broad, with fingers occupying distal third. Palm with sculpturing common for group, superior transverse groove continuous with triangular depressed areas on either face; proximal margin of groove, when seen in profile, vertical to margin of palm. Inferior lobe slightly distal to superior groove, strong, and continuing to 0.25 height of palm on outer face; rounded on inner face. Dactylus heavy, compressed, superior margin rounded. Length of merus equal to about 0.5 height of palm, outer face less than 2.5 times as long as broad; inferior internal margin sharp, bearing single movable spine in middle, and distally produced into strong, acute tooth.

Small chela 3.2 times as long as broad, with fingers occupying distal 0.5; palm proximal to adhesive plaque slightly raised, rounded, with shallow depressions on either side; no teeth about digital articulation. Dactylus slender, tapering and curved, with slight trace of setiferous expansion on proximal portion; inner face bearing knife-like ridge that meets corresponding ridge on fixed finger; knife ridges of both fingers paralleled by row of short stiff setae. Merus half as long as chela, slightly over twice as long as broad, bearing movable spine and distal tooth like that of large cheliped on inferior internal margin.

Carpus of second legs with ratio: 10:11:4.2:4.5:5.8.

Ischium of third legs bearing strong mov-

able spine; merus 4.3 times as long as broad, distally unarmed; carpus 0.5 length of merus, superior and inferior margins produced but rounded; propodus 0.7 as long as merus, bearing five strong spines on inferior margin, five smaller spines near margin, two strong spines distally. Dactylus simple, tapering, curved, 0.25 length of merus.

Telson 3.3 times as long as tip is broad, 1.8 times as broad anteriorly as posteriorly; lateral margins slightly concave in posterior third; tip broadly arcuate, larger spines about half as long as tip is broad, tip also bearing series of short spinules above bases of setose bristles; anterior pair of dorsal spines before middle.

Paratype similar to holotype in all characteristics except that length of merus of large chela is approximately equal to height of palm and relatively more slender.

DISCUSSION: The specimens in the paratypic series exhibit the normal and expected variations. In some, especially the smaller specimens, the rostrum is shorter, in one extreme case reaching only to the middle of the visible portion of the first antennular article. On the meri of both chelae the number of spines is variable, from none (especially on the smaller cheliped) to three; in one specimen, of questionable identity because it was small and broken, there are eight movable spines. The large chela itself often is somewhat more slender, in one reaching the maximum of 3.0 times as long as broad. In several specimens the tips of the fingers are calcified and white. The relative lengths of the spines on the propodus of the third legs are also variable, some being shorter and others being longer than those depicted for the type specimen. In the telson of many specimens the margins of the anterior portions are straighter and more parallel, posteriorly the margins are more deeply concave, the tip is relatively narrower.

In one female from the collection that produced the type and allotype the setae, but not the spines, of the telson, uropods and

posterior pleopods were dark, almost black, contrasting with the alcohol-bleached body.

This species plainly belongs to the Edwardsii group of the genus, and can be separated from most other members of the group by the form of the rostrum, the lack of a meral tooth, the simple dactylus of the third legs, and the simple condition of the dactylus of the small chela in both sexes. In the key of de Man (1909: 325) this species comes out to *A. haanii* Ortmann, but the two species cannot be confused because *haanii* bears deep grooves arising both medially and laterally to the orbital hoods that almost encircle the orbital hoods according to de Man's redescription of the type specimen (1897: 751); moreover, the second carpal article is definitely shorter than the first (ratio of 2.3:1.5 instead of 10:11).

This species looks very similar to the specimens which I identify as *A. leptochirus* Coutière. If it were not for the lack of the fringe of setae on the dactylus of the small chela of the male, the two would have been considered to be a single species. In fact, the great similarity renders questionable the use of this fringe of setae as a specific characteristic. However, as there is no evidence, only suspicions, about the validity of this accepted criterion, it was decided to describe this species as new.

The name is derived from the Greek doleros —deceptive.

Alpheus parvirostris Dana

Alpheus parvirostris Dana, U. S. Explor. Exped. 13: 551, pl. 35, fig. 3, 1852.

LOCALITIES: Banner, 65 specimens in 9 collections; Cloud, 2 specimens at A-5, 1 at C-7a, 6 at D-5, 2 at Loc. 6.

DISCUSSION: These specimens agree very well with the redescription given by de Man (1911: 432) and with the short original description. There are several minor but noteworthy variations, however. De Man stated that the length of the first carpal article of the

second legs was about twice the length of the second article, whereas in most of these specimens it ranges from 1.5 to 1.8 times as long. The tooth on the inferior margin of the third and fourth legs varies in its development, with that of the fourth legs at times lacking, and that of the third legs quite small; this variation appears to be roughly correlated with size, with the smaller specimens showing a poorer development of the meral tooth. Like de Man's specimens, these specimens showed variation in the relative lengths of the stylocerite, scaphocerite and especially the lateral spine of the basicerite.

Coutière's statement of distribution for this species (1905: 906), that it is found "depuis le cap jusqu'aux îles Sandwich. . . ." is not based on any other published record, and the species was not found in the extensive Hawaiian collections previously reported upon (Banner, 1953). It is likely the statement is erroneous.

THUNOR

In 1949 Armstrong (1949: 12) erected a new genus *Thunor* for the species described by Schmitt as *Crangon rathbunae* (1924: 74) from the Barbados. He separated *Thunor* from *Alpheus* (*Crangon*) primarily on the basis of four characteristics: 1, The obsolescence of the ocular beak, the anterior projection arising between the bases of the eye stalks. 2, The absence of the cardiac notch, a notch on the posterior margin of the carapace between the attached dorsal region and the bases of the branchiostegites. 3, The lack of anal tubercles, projections on the ventral side of the telson flanking the anus and engaging the inner uropods. 4, The absence of a transverse articulation on the outer uropod. There were also two other characteristics that Armstrong evidently considered as less important: The rostrum was absent and the outer branch of the palp of the first maxilla lacked setae. Otherwise the genus was like *Alpheus* with the large chela like that of the Obesomanus group; moreover, the type species, *T. rath-*

bunae has an elongation of the antennular peduncle and the extreme reduction of the parts of the antennal base that is also common in the *Obesomanus* group. Armstrong felt that *T. rathbunae* was most closely related to *A. idiocheles* Coutière (printed *idocheles*, *lapsus calumi*), an unusual species that Coutière placed in the *Megacheles* group with doubts. These two species are closely related; as I am tentatively accepting *Thunor* I am transferring the species *idiocheles* to this genus and adding another species here referred to as *T. species 1*.

To review the validity of this separation I have examined specimens that I consider to be related to *T. rathbunae*, to *T. idiocheles* or to the *Obesomanus* group. These include specimens identified as *T. idiocheles*, *A. lutini* Coutière, *A. microstylus* (Bate), *A. phrygianus* Coutière, *A. perplexus* and *A. chamorro* and three specimens, possibly belonging to new species, too incomplete for specific identification, *A. species 2*, and *T. species 1*. The characteristics of these species are discussed in their individual sections; here only the way they meet the criteria of Armstrong is considered.

1. The ocular beak. As this characteristic is impossible to see unless the specimen is either distorted in capture or the intact specimen torn apart, I do not feel inclined to ruin one of the small number of specimens representing some species. The character was not examined in *A. lutini*, *A. perplexus*, *A. chamorro*, and *A. species 2*, in the others it is as follows:

T. idiocheles and *T. species 1*—lacking.

A. microstylus—present but poorly developed.

A. phrygianus—present, of moderate development.

2. The cardiac notch. In most specimens this characteristic is difficult to discern because the posterior margin of the carapace is not well defined, and, being transparent, tends to be indistinguishable from the opaque white of the underlying tissues.

T. idiocheles, *A. lutini*, *microstylus*, and *chamorro*—cardiac notch present.

A. phrygianus—cardiac notch lacking, but dorsal region set off from brachiolegites by an angle.

A. species 2—region rounded where cardiac notch should occur.

T. species 1—slightly developed cardiac notch in male, margin without notch but angular, not rounded, in female.

3. The anal tubercles. In those species in which they are present, they are well developed in the form of a small papillose structure; otherwise there is no vestige of them.

T. idiocheles, *T. species 1*—lacking anal tubercles.

A. lutini, *microstylus*, *phrygianus*, *perplexus*, *chamorro*, and *A. species 2*—anal tubercles present.

4. Articulation of the outer uropod. Often this is difficult to see in preserved specimens. It can best be checked by bending the tip of the uropod ventrally and noting whether it bows in a rounded fashion or bends sharply along the line of articulation.

T. idiocheles, *T. species 1*—without articulation.

A. lutini, *microstylus*, *phrygianus*, *perplexus*, *chamorro*, and *A. species 2*—with articulation.

In this series of species, e.g., *A. species 2* and *T. species 1*, as well as those previously reported, e.g., *A. microstylus*, the presence or absence of the rostrum is variable within the species. In no specimens were the maxillae examined.

To recapitulate Armstrong's criteria: the ocular beak as the basis for working separation appears to be valid but impractical, especially where only a few specimens are available; the cardiac notch appears to be too variable; leaving for the separation of the two genera only the two characteristics, the anal tubercles and articulation of the uropods. If this separation is made, then *T. idiocheles*, and *T. species 1* belong to *Thunor*.

Opposed to this separation would be a series of characteristics, for the species agree well with *Alpheus* for the most part. The ex-

treme form of the rostral front of *T. rathbunae* is approached in a number of species plainly belonging to *Alpheus* (including *A.* species 2); the peculiar development of the antennules and antennae is approached by many species of the *Obesomanus* group; the large and small chelae are similar to those found in the *Obesomanus* group; there is nothing in the second and subsequent thoracic legs and pleopods that would serve to separate the two genera; even the brachial formula is the same.

I, therefore, am in doubt as to the validity of this separation, and believe that at most the species of *Thunor* should be put into a group or subgroup within the genus *Alpheus*. However, until more closely related species are examined in reference to these differences and similarities in order to better determine the constancy of the differences, I will recognize the genus *Thunor*.

Thunor idiocheles (Coutière)

Fig. 22

Alpheus idiocheles Coutière, Fauna and Geog. Mald. and Laccad. 2(4): 883, pl. 75, fig. 21, 1905.

LOCALITIES: Banner, 5 specimens in 4 collections; Cloud, 1 specimen at locality D-7.

DISCUSSION: These specimens agree very well in almost all characteristics with those in Coutière's description. However, there are some variations that should be noted. The rostrum is found to vary slightly in proportions, from a slight triangle to one that reaches as far anteriorly as the rounded anterior end of the stylocerite. In all specimens the rostral carina is marked. The carpocerite and lateral spine of the scaphocerite in one specimen are equal in length to each other and reach only to the end of the second third of the second article of the antennular peduncle, in other specimens they are unequal with the carpocerite only reaching to the end of the second antennular article, and in one specimen the spine of the scaphocerite reaches to the end of the second antennular article and the

carpocerite exceeds it, reaching almost a third the length of the third antennular article. Of the four specimens which retain a large chela, three have a length-breadth ratio of 3, instead of 3.5 as reported by Coutière. The telsons are quite variable, and in none were the posterolateral spines as poorly developed as those shown by Coutière. Finally, four of the six specimens have a strong brown spine on the external margin of the outer uropod; the other two have more slight and colorless spines; in none are there two short brown spines as described by Coutière.

Two of the specimens have such markedly dissimilar telsons that they were originally thought to be of a different species. These are the specimens illustrated in the figures. Unfortunately neither specimen has its large chela intact. However, as they agree very well otherwise with intact specimens identified as this species, and as the telsons of the four intact specimens are also variable, it is thought that this difference probably is not of significance. Similar wide variation has been reported by Armstrong in *Thunor rathbunae* (Schmitt).

Coutière did not remark upon the lack of an articulation in the outer uropod, and, to the contrary, he showed a line that could be interpreted as an articulation in his figures. None of the Saipan specimens has an articulation although some show a slight line starting transversely from the region of the lateral spine, similar to that shown by Coutière. This faint line, possibly a rudimentary articulation, does not reach to the opposite margin in any specimen.

The cardiac notch of the carapace is present and the anal tubercles are lacking in all specimens.

Thunor species 1

Fig. 23

SPECIMENS: An 8.5 mm. male (carapace length 3.7 mm.) lacking large and small chelae, and one of each pair of posterior

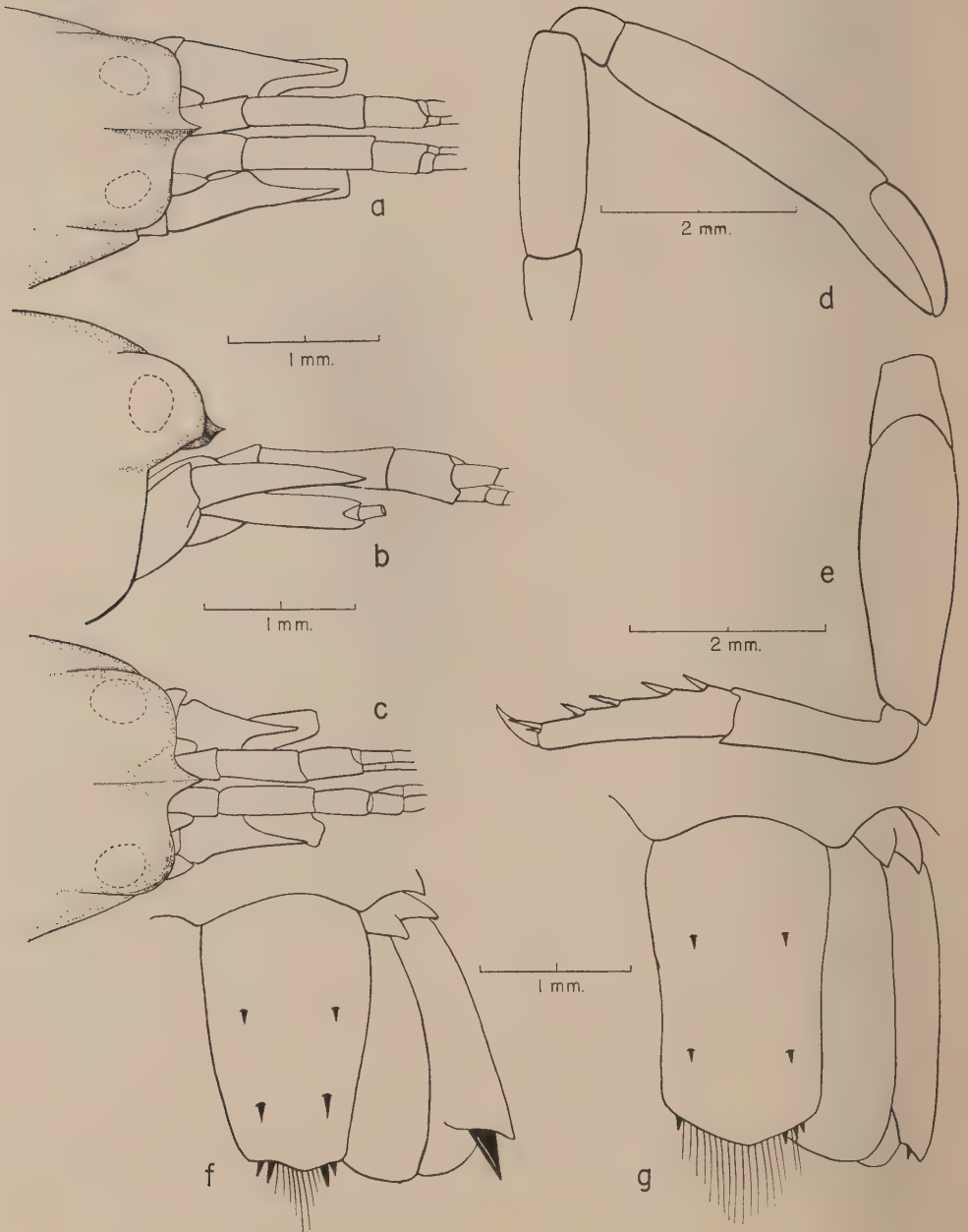


FIG. 22. *Thunor idiocheles* (Coutière), aberrant specimens. *a, b*. Anterior region, dorsal and lateral aspects, male; *c*, same, female; *d*, small cheliped, female; *e*, third leg, male; *f*, telson and uropod, male; *g*, telson and uropod, female.

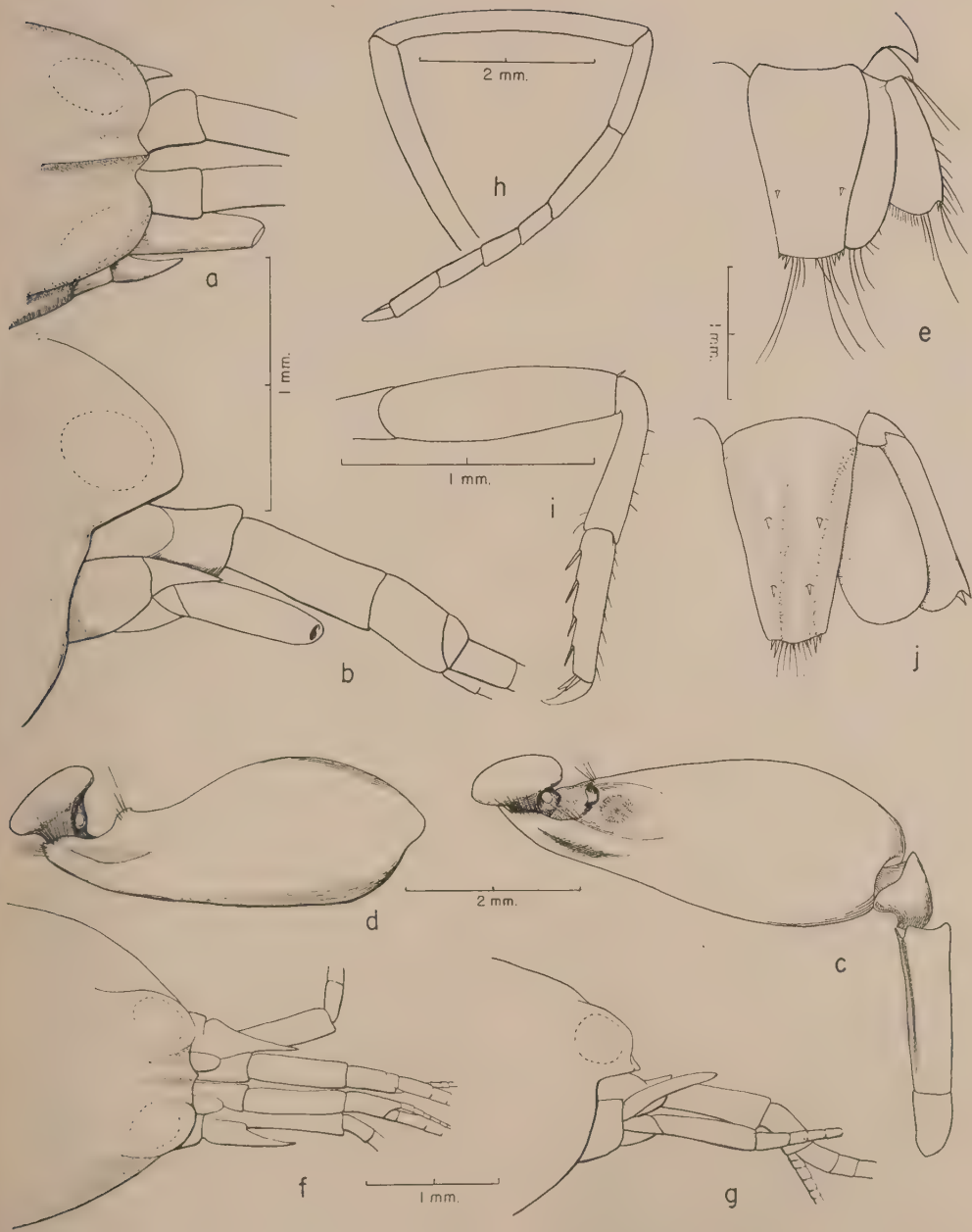


FIG. 23. *Thunor* species 1. *a-c*. Female: *a*, *b*, anterior region, dorsal and lateral aspects; *c*, *d*, large cheliped; *e*, telson and uropod. *f-j*. Male: *f*, *g*, anterior region, dorsal and lateral aspects; *h*, second leg; *i*, third leg; *j*, telson and uropod.

thoracic legs; a 10.4 ovigerous female (carapace length 3.9 mm.) lacking all thoracic legs except the large chela, basal articles of 2nd and 4th legs, and 5th legs. Specimens collected at the same time by A. H. Banner.

DESCRIPTION: Body heavy, with cephalothorax markedly heavier than abdomen; thoracic legs long and heavy. (Because of the differences between the male and the female the descriptions will be given separately.)

Male. Anterior carapace rounded and depressed in lateral view. Orbital hoods inflated, rounded anteriorly, and higher in lateral view than interorbital area. Rostrum small, triangular, acute, and bearing a low but sharp carina that extends posteriorly to behind orbital hoods. Margin of carapace between anterior orbital hoods and rostrum almost straight.

Antennular peduncle long and slender, with second article 4 times as long as broad and about twice as long as visible portion of first and third articles (third article slightly longer than first). Stylocerite rounded, reaching only 0.5 length of visible portion of first article. Outer flagellum 1.1 times as long as peduncle, inner flagellum slightly longer than outer.

Basicerite unarmed. Scaphocerite reduced, with tip of lateral spine reaching only to middle of second antennular article; blade almost rudimentary, reaching only to end of first antennular article. Carpocerite reaching end of second antennular article. Flagellum long, about 2.5 times as long as outer antennular flagellum.

Carpal articles of second legs with the ratio: 10:12:4.5:5.2:6.0. Chela as long as basal carpal article, with fingers occupying only distal 0.3.

Third legs with ischium unarmed. Merus unarmed, 3.5 times as long as broad. Carpus with superior distal margin projecting as a heavy rounded tooth, inferior margin unarmed; 0.57 as long as merus. Propodus 0.64 length of merus, 4 times as long as broad proximally, and tapering distally; armed with four strong spines on inferior margin and two

distally. Dactylus simple, curved, slightly less than 0.3 the length of propodus.

Pleura of anterior abdominal somites rounded. Uropods of usual form and armature except strong spine of outer uropod brown and outer uropod without trace of distal articulation. Telson 4.0 times as long as posterior margin is broad, 2.5 times as broad anteriorly as posteriorly; lateral margins almost straight, posterior lateral corners rounded, posterior margin slightly arcuate. Anterior pair of spinules 0.4, posterior pair 0.7 of length of telson posterior of articulation; posterior lateral pairs of spinules of moderate development; central tuft of setae of usual form but short, and telson bearing at bases of setae a series of short spinules. Dorsal surface of telson without usual uniform convexity, but bearing two low rounded ridges that merge anteriorly.

Female. Orbital hoods similar in form to those of male. Rostrum slightly asymmetrical, rounded; dorsal carina higher and more rounded than in male. Margin of carapace between orbital hoods and rostrum not straight but with rounded and asymmetrical indentations.

Antennular peduncle similar to that of male except stylocerite concealed by carapace in dorsal view. Flagellar lengths about same as in male.

Basicerite unarmed, rounded. Scaphocerite extremely reduced, a simple, heavy, acute triangle, with tip reaching almost to end of first antennular article. Carpocerite reaching only slightly past middle of second antennular article. Flagella broken.

Large chela slightly compressed at base, with rounded margins; 2.7 times as long as greatest width, strongly tapering towards fingers. Dactylus hammer-shaped, with length of "head" about 0.2 length of entire chela. Fixed finger rounded, hardly extending beyond articulation of dactylus, much shorter than dactylus and not meeting in apposition. Palm of large chela with two rounded ridges distally leading towards palmar adhesive plaque; adhesive plaque borne on eminence

that is proximally delimited by deep, rounded concavity that accommodates end of "head" of dactylus when dactylus is flexed. Palm also bearing shallow, triangular depression or groove near dactylar articulation; corresponding area on inner face marked by much less extensive depression. Merus of cheliped 4 times as long as outer face is broad, unarmed.

Outer uropod short, abruptly truncate; spine at termination of outer shoulder poorly developed; ramus with small distal triangle that appears to have resulted from a fracture, not an articulation; tip bearing only few long setae. Inner uropod of usual form but with only occasional long setae. Telson 2.9 times as long as tip is broad, 1.8 times as broad anteriorly as posteriorly; lateral margins anteriorly convex, posteriorly slightly concave, slightly asymmetrical; posterior lateral corners rounded; tip very slightly arcuate; superior surface smooth, armed with but a single pair of spines of feeble development located 0.7 of the length posterior to articulation; on tip three pairs of spines and two pair only of long setae adjacent to spines, three shorter setae on left, two on right, middle of tip devoid of all setae.

Eggs without developing larvae, subspherical, 0.6 mm. diameter.

DISCUSSION: These two fragmentary specimens are perplexing. The question arises as to whether they are of the same species. The general form of the anterior carapace, the antennules, the few appendages that they have in common, are similar, yet there are marked differences in the rostrum, in the scaphocerite and especially in the telson and uropods. Unfortunately, because of the fragmentary condition of the specimens, comparison cannot be made in the thoracic legs. In view of the considerable variation that has been noted in the species of *Thunor* and in related Obesomachus group of the genus *Alpheus*, in view of the general similarities noted, and especially in view of the fact that this pair, male and female, were collected together and may have been therefore a cohabiting pair, I be-

lieve that they represent a single species and their differences are individual variations.

The lack of anal tubercles and the lack of the articulation on the outer uropod place this species in the genus *Thunor*. These two fragmentary specimens can be distinguished from *T. idiocheles* (Coutière) in the proportions of the antennular peduncle, the greater reduction of the scaphocerite and, most important, in the depression on the palm of the large chela behind the dactylar articulation and the pronounced hammer-shape of the dactylus of this appendage. This species can be distinguished from the Caribbean *T. rathbunae* by the presence of a rostrum. Another specimen of this species, more complete, is available in another collection, and with that as the type the species will be described and named in a later paper.

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- ³ In my 1953 paper (p. 1) I noted that Haskell, in his study of the reports of the U. S. Exploring Expedition, considered that February, 1853, was the official date of publication of Dana's volume on the Crustacea. L. B. Holthius has pointed out to me in a personal communication that this is only the date that the U. S. Printing Office delivered 58 official copies of the work to the Department of State, and that the unofficial copies must have been distributed earlier, for the *American Journal of Science* (Ser. 2, 15: 466, 1853) acknowledges the receipt of this volume in December, 1852. Therefore the generally accepted date of publication, 1852, is the correct one.
- Dr. Holthius also pointed out that the part of volume 6 of the proceedings of the Academy of Natural Sciences, Philadelphia, that carries Dana's "Conspectus Crustaceorum etc.", and which bears the volume date of 1854, must have been published by May, 1852 (*op. cit.* 6(3): 71, 72), so for questions of priority for Dana's species, this earlier date should be used.
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The Origin of the Spermatophoric Mass of the Sand Crab, *Hippa pacifica*

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SUMMARY

1. In *Hippa pacifica*, mitotic division of germinal epithelial cells produces primary spermatocytes which, as sustentacular-like cells appear, divide meiotically to form spermatids.

2. Concurrently as spermatids metamorphose into spermatozoa, germinal epithelial cells renew their activity and again produce primary spermatocytes which, as they fill the sacculus, expel the spermatozoa.

3. A continuous spermatogenic mass enters the vas deferens, where an enveloping secretion from the epithelial cells bounding the lumen forms a thin sheath to the sperm mass.

4. The lumen (viewed in cross-section) becomes keyhole-shaped and a secretion from a wedge-shaped group of cells bounded by two deep crypts both surrounds the sheathed sperm mass and forms a ribbon-like supporting stalk and a broad, basal foot.

5. As the lumen again becomes circular (in cross-section), a secretion from the epithelial cells surrounds the completed spermatophore and forms the homogeneous matrix.

6. The spermatophore of *H. pacifica* is both macruran-like, because of its continuous, highly convoluted sperm mass, and anomuran-like, because of its raised spermatophore and broad foot.

7. Neither the anomuran-like spermatophore of a macruran, *Parrabacus antarcticus*, nor the macruran-like spermatophore of an anomuran, *Hippa pacifica*, justifies the inference that these two animals occupy a systematic position intermediate between the Macrura and the Anomura, but rather illustrates the need for consideration of many characters before postulating relationships.

INTRODUCTION

THE purpose of this paper on the origin and development of the spermatophoric mass of *Hippa pacifica* is twofold: (1) to extend our knowledge of hippid biology, and (2) to show that in *H. pacifica* the spermatophores are intermediate between the non-pedunculate macruran and the pedunculate anomuran spermatophores.

With the exception of the Cape crayfish (*Yasus lalandii*, see von Bonde, 1936) and the rock lobster (*Parrabacus antarcticus*, see Matthews, 1954a), all recorded observations indicate that the palinurids, the astacids, the homarids, and the nephropsids produce typical macruran spermatophores consisting of highly convoluted tubes embedded in sticky, putty-like matrices (*Panulirus interruptus*, see Allen, 1916; Fasten, 1917; Wilson, 1948; *P. argus*, Crawford and DeSmidt, 1923; *P. penicillatus*, Matthews, 1954c; *Potamobius trowbridgii*, Andrews, 1931; *Homarus americanus*, Herrick, 1895; *Enoplometopus occidentalis*, Matthews, 1954b).

With the exception of the hippids, all recorded observations indicate that

the galatheids, pagurids, and porcellanids produce typical anomuran spermatophores in which the continuous, convoluted tube of the macrurans is broken into distinct ampullae, elevated on peduncles attached to a foot-like base (Galatheida, Paguridae, Porcellanidae, see Mouchet, 1930-1; Paguridae, Matthews, 1953).

On the basis of anatomical characteristics, the families of the tribe Macrura are usually considered more closely related than are the families of the tribe Anomura. Since an anomuran-like spermatophore has been reported for a member of the Macrura (see papers cited by Matthews, 1954a), one might expect that a macruran-like spermatophore would ultimately be reported for a member of the more heterogeneous Anomura. This study reports such a spermatophore and points the need for the consideration of both morphological and physiological characteristics in postulating taxonomic relationships between these groups of animals.

METHODS AND TECHNIQUES

Specimens of *Hippa pacifica* (Dana) taken in the vicinity of Waimanalo Bay, Oahu, during the high surf of June 1954, were used in this study. Both males and females were taken. The ratio of males to females was 1:15. Of these, nearly all females were in the berried condition and all males over 1.5 cm long were sexually mature. The reproductive systems of non-anaesthetized males immersed in sea water were removed with the aid of a dissecting microscope.

The testes and right vasa deferentia were either fixed in Bouin's fluid, washed in alcohol (70%), cleared in dioxane, embedded in Tissuemat (54-56° C), sectioned at 10 μ , and stained in standard alum haematoxylin and eosin; or they were fixed in Champy's fluid, washed in running water (24 hours), dehydrated in alcohol, cleared in cedarwood oil, infiltrated with xylene, embedded in Tissuemat (54-56° C), sectioned at 4-6 μ , and stained in iron haematoxylin.

The left vasa deferentia were immersed for 10 to 30 minutes in an aqueous solution of toluidin blue (1:10,000) and teased open in sea water, and their vitally stained contents studied and drawn.

OBSERVATIONS

The morphology of the testes and the vasa deferentia

The mature testes freed of overlying tissues resemble an elongate H, the right and left sides being formed of whitish, sacculate tubes joined one to the other by a short transverse bridge (fig. 1, c). The anterior portion of the testis (a) exceeds the posterior portion (d) both in diameter and length, although the sacculi (b) in all regions are of approximately the same size (0.2 mm).

The proximal portion of the vas deferens (e) arises medially at the junction of the posterior horn of the testis and the transverse bridge. This rather thin, funnel-like portion gradually tapers into a minute, straight tube (f), which lies contiguous with the intestine. Posteriorly, this minute portion terminates

in two or three tightly coiled loops (*g*) demarcating the anterior boundary of the enlarged vas deferens (*h*). This portion of the vas deferens terminates on the coxopodite of the small, chelate fifth pereopod (fig. 2, *a*) in a peculiar cup-like projection (*b*), to which completed spermatophores often adhere.



FIG. 1. Dorsal view of dissected *H. pacifica* showing *a*, anterior portion of testis; *b*, sacculi; *c*, transverse bridge; *d*, posterior portion of testis; *e*, funnel-shaped portion of proximal vas deferens; *f*, minute, straight portion of vas deferens; *g*, tightly coiled loops of vas deferens; *h*, enlarged portion of vas deferens. Magnifications as indicated.

The histology of the testes and the vasa deferentia

In histological cross-sections taken through the various portions of the testis (fig. 1, *a*, *c*, *d*), sacculi (*b*) in all stages of maturity are observed. Because the process of maturation in the sacculi of *H. pacifica* so nearly approximates the process of maturation in the sacculi of a nephropsid lobster (see Matthews,

1954*b*, figs. 2, 3, 4, pp. 116-17), only a brief summary is here given. The immature sacculus of *H. pacifica* discloses large primary spermatocytes indistinguishable from the germinal epithelial cells. As the sacculus matures,

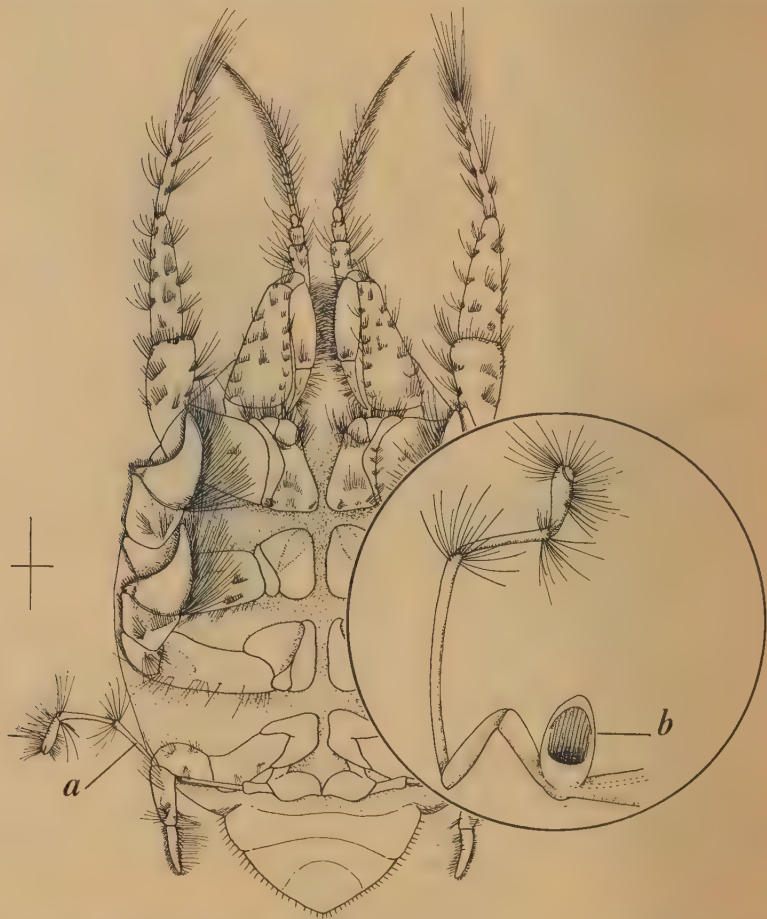


FIG. 2. Ventral view of *H. pacifica* showing *a*, small, chelate, fifth pereiopod; *b* (in enlarged insert) cup-like projection.

sustentacular-like cells with indistinct cytoplasm but strongly chromophil nuclei appear. These cells, which lie indiscriminately among the primary spermatocytes, increase in number, but both their origin and method of multiplication remain obscure. It was not ascertained whether the presence of these unique cells influences spermatogenesis, but the study of many sections reveals that as the number of these sustentacular-like cells increases, the number of secondary spermatocytes increases. Then these secondary spermatocytes divide to form spermatids.

Sections through more mature sacculi reveal that, concurrently with the metamorphosing of spermatids, germinal epithelial cells renew their activity and again produce primary spermatocytes; these, as they fill the sacculi, expel the metamorphosing spermatids.

Whereas cross-sections taken from various regions of the testis (fig. 1, *a*, *c*, *d*) are histologically similar, cross-sections taken from various regions of the vas deferens (fig. 1, *e*, *f*, *h*) are histologically different (figs. 3–15). These differences are, for the most part, due to changes in thickness of the epithelial and muscular layers, which in turn affect the size and shape of the lumina.

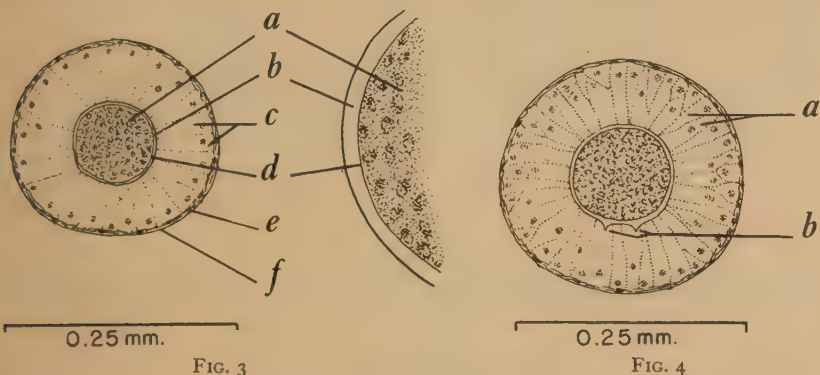


FIG. 3

FIG. 4

FIG. 3. Cross-section through the straight, proximal portion of the vas deferens showing *a*, sperm mass; *b*, lumen; *c*, epithelial cells; *d*, sheath of sperm mass; *e*, muscle layer; *f*, connective tissue layer.

FIG. 4. Cross-section through the proximal portion of the vas deferens showing *a*, epithelial cells; *b*, crypts.

Thus the lumen is a gradually changing die through which the sperm mass from the testis is moulded.

The sperm mass (fig. 3, *a*) enters the almost circular lumen (*b*) of the straight, proximal portion of the vas deferens. The lumen here is bounded by epithelial cells (*c*) whose secretion both permeates the loosely packed sperm mass and forms an extremely thin sheath to the sperm mass (*d*). The mechanism by which the sheathed sperm mass traverses the proximal portion of the vas deferens is obscure. Since the muscle layer (*e*) which lies between the epithelial (*c*) and connective tissue layers (*f*) is here poorly developed, it is doubtful if it serves either to mould the sperm mass in conformity to the lumen, or by peristalsis to force the sperm mass along. Both processes are probably accomplished in this region of the vas deferens by the continuous flow of sperm mass from the testis.

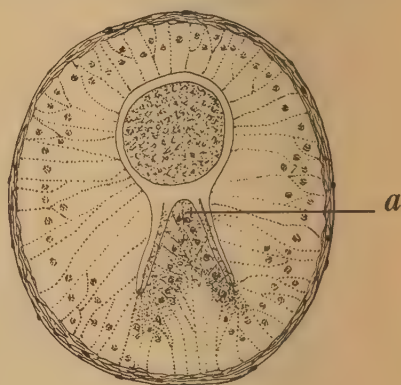
Gradually, in more distal cross-sections (fig. 4), the epithelial cells (*a*) lengthen, and two minute crypts (*b*) appear. These crypts deepen (fig. 5, *a*) and demarcate a wedge-shaped group of cells (fig. 6, *a*). Even before this wedge-shaped structure appears, its future position is indicated by a small

group of cells whose cytoplasm has an affinity for the nuclear stain, whereas the cytoplasm of other epithelial cells bounding the lumen retain their affinity



0.25 mm.

FIG. 5

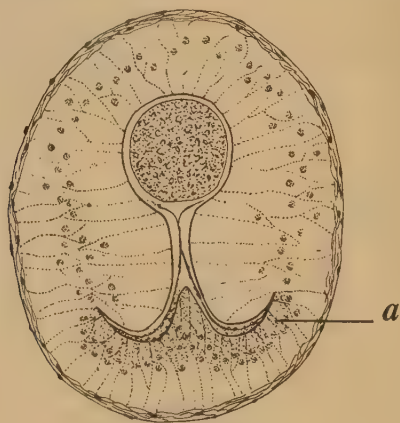


0.25 mm.

FIG. 6

FIG. 5. Cross-section through the proximal portion of the vas deferens showing *a*, deep crypts.

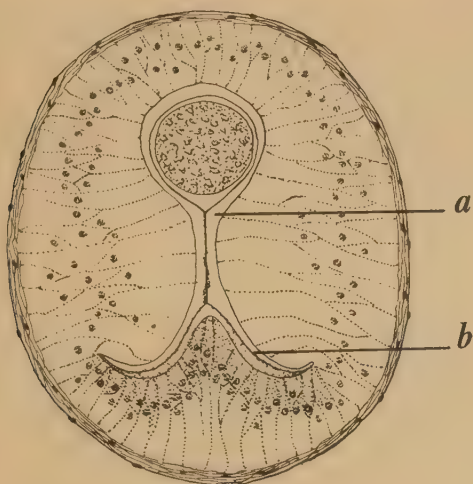
FIG. 6. Cross-section through the proximal portion of the vas deferens showing *a*, wedge-shaped group of cells demarked by deep crypts.



0.25 mm.

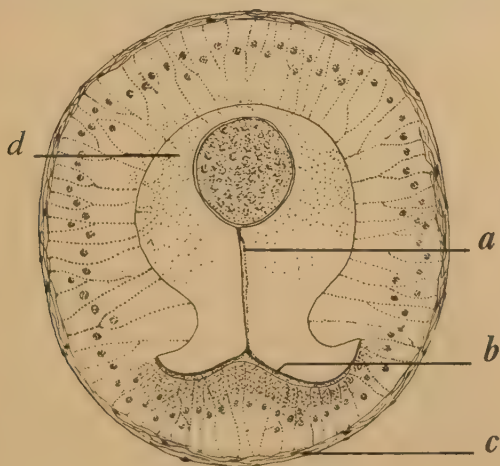
FIG. 7. Cross-section through the proximal portion of the enlarged vas deferens showing *a*, epithelial cells adjacent to wedge-shaped structure.

for the cytoplasmic stain. At first, this difference in staining reaction is limited to those cells actually comprising the wedge-shaped structure, but later, as the crypts spread peripherally forming a broad W (fig. 7), the cytoplasm of cells adjacent to the wedge-shaped structure also takes up the nuclear stain (*a*).



0.25 mm.

FIG. 8. Cross-section through the proximal portion of the enlarged vas deferens showing *a*, keyhole-shaped lumen; *b*, secretion from epithelial cells bordering W-shaped crypt.



0.25 mm.

FIG. 9. Cross-section through the proximal portion of the enlarged vas deferens showing *a*, secretion from epithelial cells bordering W-shaped crypt forming ribbon-like stalk; *b*, foot; *c*, muscle layer; *d*, matrix.

By this time a secretion (fig. 8, *b*) from the epithelial cells bordering the crypt fills the keyhole-shaped lumen (*a*) and surrounds the already sheathed sperm mass. Gradually (fig. 9) this secretion forms the ribbon-like stalk (*a*) and the

broad, basal foot (*b*). An increase in thickness of the muscular layer (*c*) suggests the possibility of muscular propulsion of the developing spermatophore, although in dissected living specimens no contractile waves of the vas deferens are observed. Still another secretion (*d*) from the epithelial cells bounding the lumen surrounds the sheathed spermatophore and forms the matrix.

In cross-sections through more distal regions of the enlarged vas deferens (figs. 10, 11) both the epithelial cells (*c*) whose secretion forms the ribbon-like stalk and broad, basal foot, and the epithelial cells (*b*) whose secretion

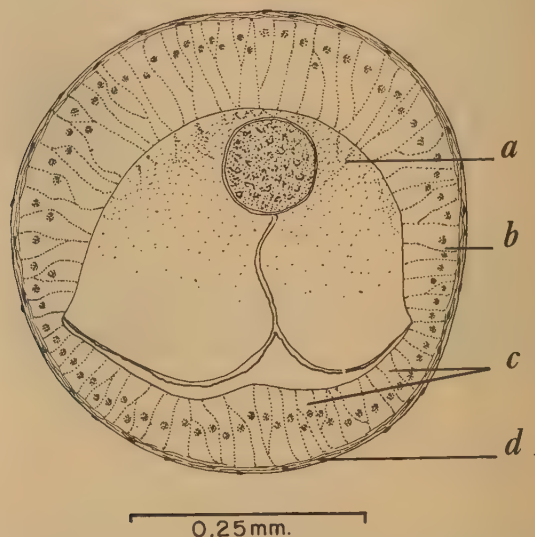


FIG. 10. Cross-section through the enlarged portion of the vas deferens showing *a*, matrix in lumen; *b*, matrix-secreting cells; *c*, ribbon-and-foot-secreting cells; *d*, muscle layer.

forms the enveloping matrix (*a*), gradually decrease in size. Since, however, the epithelial cells which lie contiguous with the foot diminish at a more rapid rate, the lumen in cross-section loses its keyhole shape and again gradually becomes more circular.

As both matrix-forming epithelial cells (fig. 12, *b*) and the foot-forming epithelial cells (*c*) diminish, the broad, basal foot (*e*) becomes widely separated from the epithelial cells (*c*). Whether this is the result of still another secretion from the foot-forming epithelial cells remains undetermined; however, a uniform matrix-like secretion now appears below as well as above the foot. Although the foot appears to be in contact laterally with the foot-forming epithelium, more distal cross-sections (figs. 13, *a*) reveal it to be free. The possibility therefore remains that, rather than another secretion, the original matrix now completely surrounds the completed spermatophore.

Since the distal portion of the vas deferens (fig. 1, *h*) is spindle-shaped, in traversing this region the completed spermatophore is crowded and the ribbon

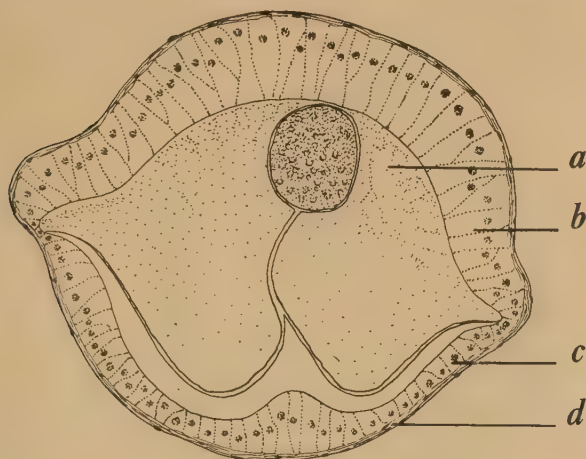


FIG. 11. Cross-section through the enlarged portion of the vas deferens showing *a*, matrix in lumen; *b*, matrix-secreting cells diminishing; *c*, ribbon-and-foot-secreting cells diminishing; *d*, muscle layer.

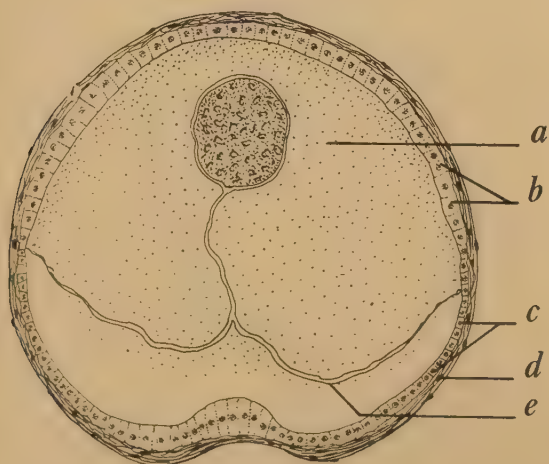


FIG. 12. Cross-section through the enlarged portion of the vas deferens showing *a*, matrix; *b*, matrix-forming cells; *c*, foot-forming cells; *d*, muscle layer; *e*, foot widely separated from foot-forming cells (*c*).

(fig. 14, *a*) is bent. The epithelium (*b*) is now an extremely small layer of cells bounding, in cross-section, an almost completely circular lumen (*c*). The circular and longitudinal muscular layers (*d*) are here well developed. The

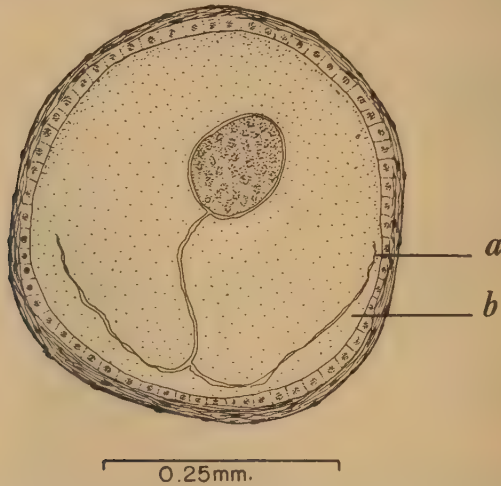


FIG. 13. Cross-section through distal portion of the vas deferens showing *a*, foot, free from foot-forming cells; *b*, matrix.

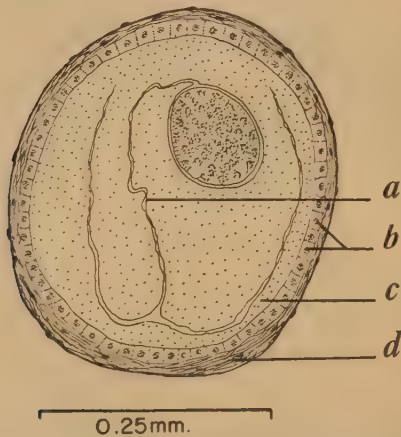


FIG. 14. Cross-section through distal portion of the vas deferens showing *a*, bent ribbon; *b*, epithelial cell layer; *c*, circular lumen; *d*, muscle layers.

latter are probably used during the actual process of spermatophore deposition.

Fig. 15 is a drawing made from a portion of the distal region of the vas deferens stained with toluidin blue and dissected to show the contained spermatophore. The encompassing matrix, which otherwise would conceal

the spermatophore, is dissolved by weak KOH. Whereas the study of cross-sections may leave some doubt as to whether the spermatophore is continuous, the study of dissected, vitally stained portions of the vas deferens leaves no doubt that the spermatophore of *H. pacifica* is a continuous, highly convoluted tube (a) raised by a continuous, ribbon-like stalk (b), attached to a broad foot (c).

Since I have not observed the attached spermatophore in nature, I cannot say whether the foot flattens or remains curved upward. This much can be said with certainty, it is the foot and ribbon which are brittle and offer sup-

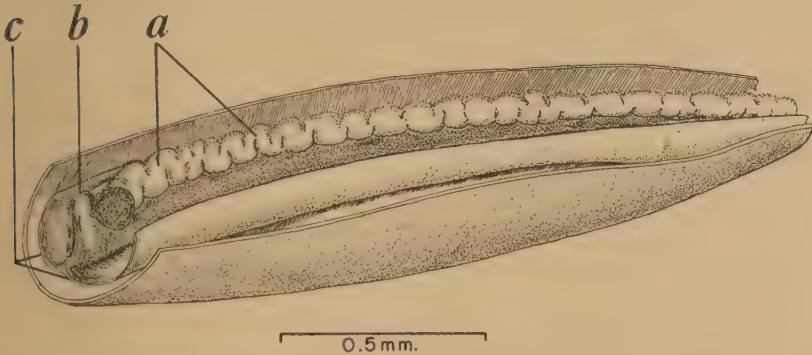


FIG. 15. Distal portion of vas deferens stained with toluidin blue and dissected showing a, convoluted sperm tube; b, ribbon-like stalk; c, broad foot.

port; the matrix, when the spermatophore is forcibly removed from the living animal, is soft and probably serves as the adhesive substance. Hardening, but no colour change of the matrix is noted. The nature of the completed spermatophore suggests mechanical liberation of spermatozoa.

DISCUSSION

Although the study of macruran spermatophores indicates that the fundamental plan is a highly coiled spermatophoric tube embedded in a homogeneous putty-like matrix, nevertheless, as previously stated, an anomuran-like spermatophore has been described for a member of the Macrura (*Parribacus antarcticus*, see papers quoted by Matthews, 1954a). This disclosure alone has little meaning except, perhaps, to point out that factors effecting change are not uniformly expressed in all organ-systems of even closely related animals. This applies to both the Anomura and the Macrura. Recent studies (in press) on the spermatophores of the land crabs *Coenobita* and *Birgus* illustrate the same point. These animals, although remarkably adapted for a terrestrial habitat, still rely on a reproductive system keyed to an aquatic (marine) environment.

Although the study of anomuran spermatophores indicates that their basic plan is a discontinuous spermatophoric tube (with ampullae of sperm) raised on slender stalks attached to a base-like foot, variations on this plan should be

expected in such a diverse group. That *H. pacifica* produces a spermatophore midway between those of the *Macrura* and the *Anomura* is, when taken by itself, of no great significance. It merely serves to illustrate that when more is learned concerning both the anatomy and physiology of organ-systems, many old-established lines of relationship may perhaps be cut across. At the present state of our knowledge concerning *H. pacifica* it is wrong to refer to this animal as crab-like, solely because of the development and position of its abdomen; and it is equally wrong to refer to it as lobster-like, solely because of the macruran nature of its spermatophore.

This paper forms Contribution No. 80 of the Hawaii Marine Laboratory.

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Method for Predicting Amount of Strontium-89 in Marine Fishes by External Monitoring

If the total radioactivity in a whole fish could be determined by means of external monitoring, this information would be very useful to ecologists, fisheries biologists, and others. If such a method were found to be suitable for field work, it conceivably could eliminate much tedious dissecting, ashing, and counting procedures. During the course of some experiments on the uptake, accumulation, and loss of radiostrontium by marine fish, a record was kept of the counts per minute detectable at various external parts of the fish's body prior to dissection and analysis of the organs and tissues by conventional ashing and counting techniques. It was not known in advance whether or not these measurements would have any significance, but the possible occurrence of a direct relationship between some aspect of external monitoring and the total amount of radioactivity in the entire fish seemed worth investigating (1).

Several species of pelagic fish, including the black skipjack tuna (*Euthynnus yaito*), the yellowfin tuna (*Neothunnus macropterus*), and the dolphin (*Coryphaena hippurus*), were fed radioactive strontium-89 in gelatin capsules. The fish were kept in tanks with circulating sea water and were killed at intervals up to 27 days. A piece of pliofilm (Saran wrap) was used to cover the fish, and the probe of a count rate meter was used to determine the number of counts per minute on direct contact. The G-M tube used had a window thickness of 3.5 mg/cm², but it was protected by a screen that reduced its efficiency to some extent.

The various organ systems and tissues of the fish were subsequently analyzed for radioactivity. The total radioactivity

recovered in each system—for example, the gills, axial skeleton, muscle—was then compared with the counts per minute (at 5-percent statistical error) that were previously found by monitoring the mouth, eye, operculum, gills, dorsal integument, and the pectoral, dorsal, and caudal fins. No apparent relationship was observed between any two parameters except that between the amount of radioactivity in the skeleton and the counts per minute found by monitoring the caudal fin. Figure 1 shows that the relationship between the number of microcuries of radiostrontium in the skeleton and the counts per minute in the caudal fin is approximately linear. Since about 30 percent of the radiostrontium found in the fishes after 7 hours occurs in the axial skeleton (2), it is therefore possible by measuring the counts per minute in the caudal fin to predict the total amount of radiostron-

tium in the entire fish.

This method proved successful only when the axial skeleton was found to have a radiostrontium content in excess of an undetermined threshold. Thus, a fish having 0.16 μC Sr⁸⁹ in its skeleton showed only background radiation with the count rate meter, but a fish with 0.40 μC Sr⁸⁹ had sufficient external radiation to be detected. The minimum Sr⁸⁹ skeletal constant is therefore somewhere between 0.16 and 0.40 μC and probably represents the loss owing to self-absorption of the beta-particle energy. These values are, of course, valid only for the particular counting system used in this series of experiments. It is possible to make the detection system considerably more sensitive and, therefore, reduce the threshold value for skeletal strontium.

The afore-described method has not yet been tried with other fission products, and in particular, mixed fission products, such as might be encountered in an area following an atomic detonation or in a region into which nuclear power plant wastes are introduced. If a parameter such as that indicated in this paper could be used to predict the total amount of radioactive material in marine fish, it might be feasible to monitor a catch on the fishing vessel or at the canning factory and, thereby, possibly prevent radioactive fish from being consumed.

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9 August 1956

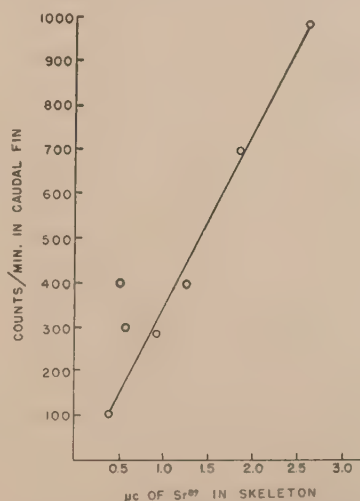
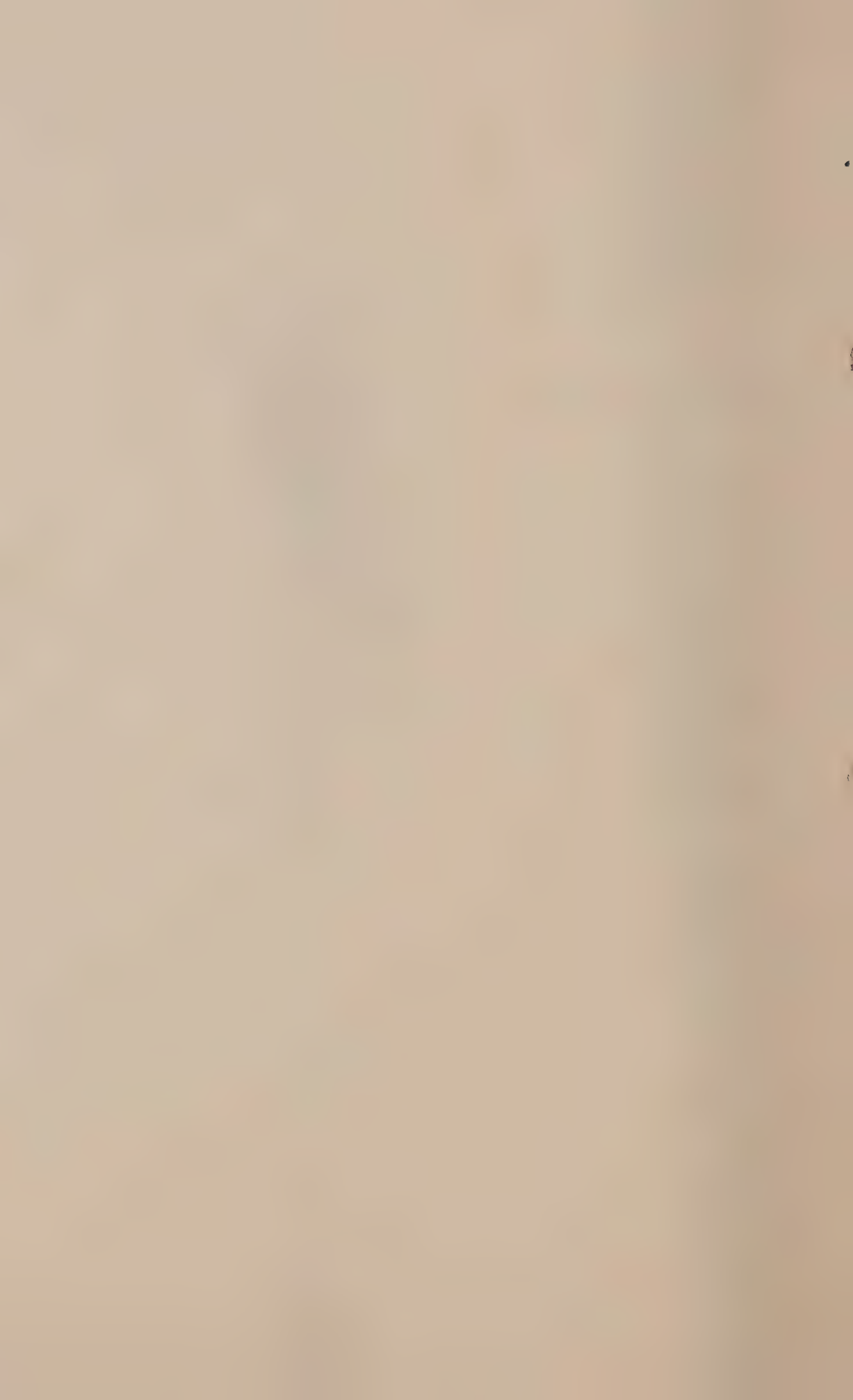


Fig. 1. Linear relationships between the counts per minute monitored in the caudal fin of tuna fed Sr⁸⁹ and the microcuries of Sr⁸⁹ found in the skeleton.



THE METABOLISM OF RADIONUCLIDES BY MARINE ORGANISMS.
I. THE UPTAKE, ACCUMULATION, AND LOSS OF
STRONTIUM ⁸⁹ BY FISHES

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Reprinted from BIOLOGICAL BULLETIN, Vol. 111, No. 3, 336-351, December, 1956
Printed in U. S. A.

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The revolution in biology which occurred about twenty years ago as a result of the utilization of isotopes has led to some problems which could hardly have been foreseen at the time. Biologists can no longer use radioactive material simply as a tool with which to solve specific problems; they are now forced to consider the effects of radioactivity which is introduced beyond their own control into an environment which they are studying. This becomes particularly important to marine and fresh water biologists who are interested in physiological or ecological problems which may be influenced in certain regions by an increase in radioactivity above the background which existed before the first atomic detonation at Alamogordo in 1945.

The weapons testing program of several nations, regardless of the type of blast, has increased the radioactivity of the seas. Underwater detonations, of course, contribute the largest percentage of their radioactivity directly to the water, but most of the fall-out from aerial bursts can be expected to appear ultimately in the ocean, since the land area of the earth is only about 30 per cent of the total. Run-off from the land will also increase the radioactivity of the seas. Far more important than the radioactivity which appears as a result of weapons testing, however, is the radioactivity which inevitably will be introduced into the oceans from nuclear power plant wastes and atomic-powered ships.

There are several important reasons for studying the metabolism of fission products and other radionuclides in marine organisms. First, several fission products are known to be potential hazards from a public health standpoint (N.B.S. Handbook 52). Second, almost nothing is known about the metabolism of these radioelements by marine species. Third, we cannot tell at present what potential ecological effects may be brought about through the deleterious action of radiation on the marine biota, but the possibility exists that some adverse changes, such as those which apparently occurred in White Oak Lake (Krumholz, 1956), might occur in estuaries and other inshore regions. It is therefore important to study these problems now, before the oceans become polluted with radioactivity, because the changes which may occur will be irreversible at least for several centuries.

The problems raised by the above considerations can best be solved by studying the metabolism of these radionuclides not only in individual organisms, but also in relation to the various trophic levels by way of the food chains. As desirable as such studies may be, it is impossible to undertake investigations of this magnitude

¹ This work was carried out with the aid of Contract No. AT(04-3)-56 between the U. S. Atomic Energy Commission and the University of Hawaii.

² Contribution No. 82, Hawaii Marine Laboratory, University of Hawaii.

for the entire marine biota. Thus, because of our special facilities at the Hawaii Marine Laboratory, we have confined our research to fishes which are representative of three distinct marine habitats, and include herbivores belonging to the second trophic level, and carnivores from the third and fourth trophic levels.

Strontium was selected for our initial studies for two reasons. First, it is chemically similar to calcium, and is therefore a "bone seeker." As such, if radioactive, it may interfere with the blood cell formation of many animals. Second, Sr^{90} has a half-life of about 28 years, so that the deposition of an atom of Sr^{90} into a tissue which has a slow rate of turnover may result in radiation exposure for the entire life of the animal. These characteristics make radiostrontium a particularly hazardous fission product. In these experiments we have used Sr^{89} because of its much shorter half-life (~ 53 days) which decreases the danger of contamination in the laboratory.

The particular objective of the present study was to measure the uptake, accumulation, and loss of radiostrontium by the various tissues and organs of selected species of fish when the isotope was given orally, by intramuscular injection, and by the immersion of the fish in sea water enriched with Sr^{89} .

MATERIALS AND METHODS

The large pelagic fishes used in these experiments consisted of the black skipjack (*Euthynnus yaito*), the yellowfin tuna (*Neothunnus macropterus*), and the so-called dolphin (*Coryphaena hippurus*). These species are fast-swimming, wide-ranging carnivores which occupy the fourth trophic level. Among the small fish used, the papio (*Carangoides ajax*), and the aholehole (*Kuhlia sandvicensis*), are small carnivores common along the reefs and shores in the Hawaiian Islands and occupy the third trophic level primarily. The aholehole is also able to adapt itself to brackish water environments, and has even been found well into fresh water streams (Tester and Takata, 1953; Tester and Trefz, 1954). The third small species used, *Tilapia mossambica*, is a sluggish fish, predominantly herbivorous, but facultatively omnivorous, and may be placed in the second trophic level. It prefers brackish water, but is well adapted to either fresh water or sea water.

Carrier-free strontium⁸⁹ was obtained from Oak Ridge and fed to the large fishes by filling gelatine capsules with cracker crumbs and a measured quantity of the isotope solution. The capsule was sewn into a small piece of fish muscle which was held just under the surface of the water by a weak thread. As the fish swallowed the bait, the thread was broken off. In this way the capsule could be given to a particular fish. In some instances small fishes were force-fed a gelatine capsule prepared in the same way. Others were fed by incorporating a measured amount of Sr^{89} into a gelatine solution which was allowed to solidify in a small plastic tube. The tube was put into the fish's stomach and the gelatine was extruded with the aid of a syringe. A dose solution was prepared by extruding the same quantity of radioactive gelatine into a volumetric flask.

The large fish were perfused with a mixture of two parts sea water and three parts distilled water. The brain, eyes, spinal cord and integument were removed, and the excised internal organs were further soaked in distilled water until no blood was apparent in the water. All the rinsings were added to the blood. The gut was opened, and any material remaining in it was flushed out. Only the eyes and

the visceral organs were removed from the small fish which were not perfused.

The remainder of the fish, consisting of muscle and skeleton for the large fish, or muscle, skeleton and integument for the small fish, was then put in a pressure cooker, brought to 20 pounds pressure and allowed to cool. After this treatment, the muscle was easily removed from the bones, and any flesh remaining on the gill arches was removed with warm formamide. Control experiments indicated that no leaching or loss of strontium occurred as a result of the pressure cooker treatment.

Wet weight of organs was obtained without blotting, and the tissues were dried at about 110° C. for 48 hours. The dried tissues were put in a muffle furnace which was brought to about 550° C. The furnace was then shut off and the samples left overnight. A slow stream of air was introduced in the oven to aid combustion.

The ash was ground and spread evenly on aluminum planchettes with the aid of water and a detergent, and dried under infra-red lamps. The samples were

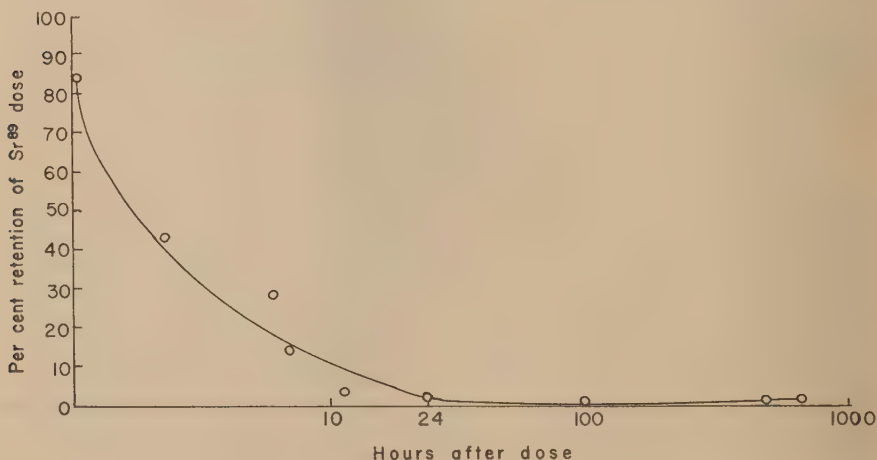


FIGURE 1. The decrease of ingested Sr^{90} in pelagic fishes as a function of time.

counted in triplicate when possible, using commercial counters and scalars. A minimum of 2560 counts was taken on each sample, including background. No corrections were made for back-scatter, self-scatter, or self-absorption. The latter is very small at the ash densities which were used ($< 5 \text{ mg./cm.}^2$). The scalars were calibrated daily with Bureau of Standards nuclides, and the only correction applied was for radioactive decay. The counts/minute of the samples were compared with aliquots of the actual dose given in each instance. Specific details for each experiment will be described at the appropriate place.

RESULTS AND DISCUSSION

A. Ingestion of Sr^{90} by large pelagic fishes

Figure 1 shows that the excretion of a single dose is very rapid: about 50 per cent disappeared within a few hours, and only 1–2 per cent was left after 24 hours. This latter value persisted for the remainder of the experiment which lasted 27 days.

Table I shows the distribution of the Sr^{89} in the various organs and tissues of these fishes, and Figure 2 is a graph showing some of these data. This graph is presented as the percentage of radioactivity of the different organs and tissues in terms of the total radioactivity found in the entire fish when it was killed. It is

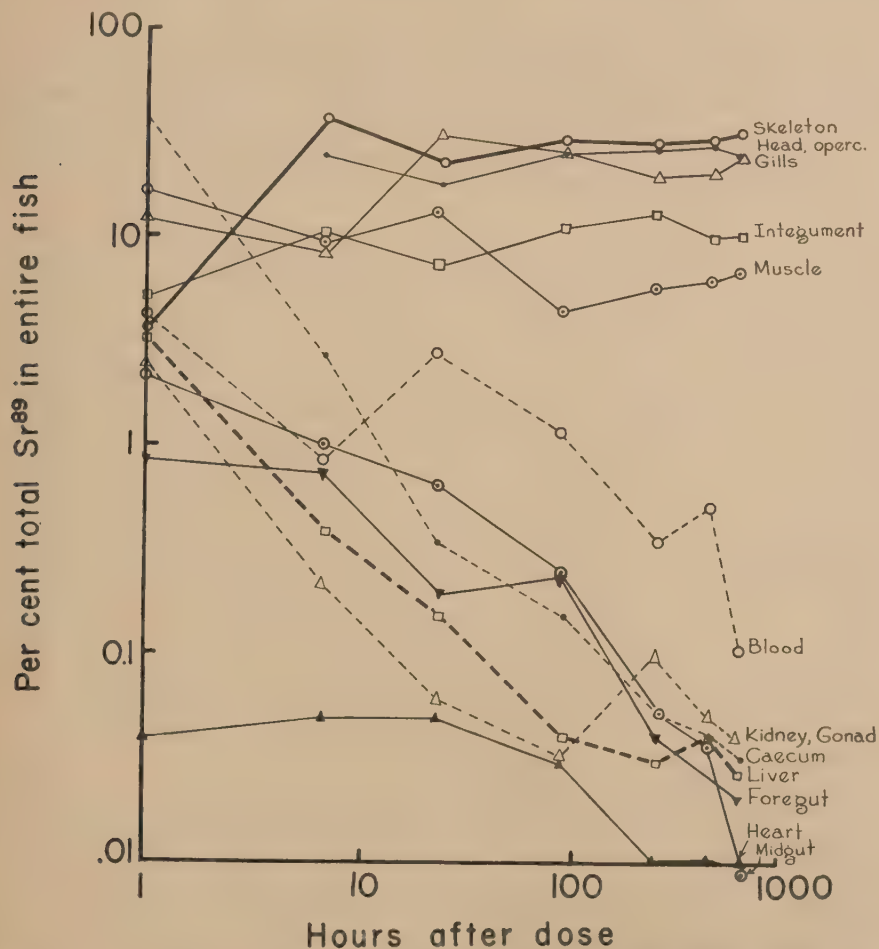


FIGURE 2. The distribution of a single ingestion of Sr^{89} in organs and tissues of pelagic fishes as a function of time.

apparent that the tissues are segregated into two groups with regard to strontium retention: the visceral, and the structural. The visceral organs and tissues, including the blood, kidney, foregut, midgut, hindgut, spleen, liver, caecum and heart, show a continuing decrease in radioactivity beginning one hour after the administration of the dose. The structural tissues, including the skeleton, head and

opercular bones, gill arches, integument and muscle appear to concentrate strontium rapidly to a level which is maintained more or less constant for a relatively long period of time. The turnover or excretion of strontium in these structures is therefore slow.

TABLE I

Accumulation of ingested Sr^{90} in the various organs and tissues of pelagic carnivorous fishes expressed as percentage of total activity

Tissue	Species	EY ¹	EY	EY	CH ²	EY	EY	EY	NM ³	EY	EY
	Dose in μ c	5.55	480	240	51.0	240	464	464	464	371	371
	Duration in hours	1	2½	6	7	11½	24	96	264	480	648
Heart		0.04	0.01	0.03	0.049	0.11	0.05	0.028	0.01	0.014	0.007
Gall bladder		0.05	0.04	0.07	0.10	0.08	0.03	0.0001	0.01	0.004	0.002
Blood		4.21	6.68	15.00	0.85	8.07	2.73	1.14	0.35	0.51	0.12
Gill flesh			0.18	0.91		5.06			2.42	1.42	2.21
Gill bone		12.44	1.34	6.47	8.56	26.39	30.61	25.72	16.80	19.48	22.76
Caecum		37.01	7.67	7.84	2.70	2.64	0.34	0.15	0.05	0.04	0.029
Foregut		0.89	9.32	1.12	0.74	1.03	0.20	0.24	0.04	0.04	0.018
Midgut		2.28	14.16	16.50	1.08	1.48	0.65	0.25	0.05	0.036	0.003
Hindgut		11.78	3.98	21.26	2.26	0.11	0.15	0.024	0.03	0.015	0.016
Gut contents		—	48.32	12.73	0.056	19.65	—	0.10	0.013	—	0.0008
Head, operculum		—	0.41	1.09	24.99	6.28	18.33	24.58	28.18	29.91	24.58
Appendicular skeleton		3.60	0.40	1.19	36.21	8.45	23.69	30.32	29.15	30.47	31.43
Liver		3.34	1.48	3.04	0.39	2.46	0.15	0.04	0.03	0.04	0.027
Spleen		0.20	0.32	1.39	0.08	0.60	0.03	0.008	0.03	0.010	0.003
Tail		—	0.42	0.15	—	0.00	—	—	—	—	—
Brain, spinal cord			0.00	0.01		0.05			1.33	0.030	0.004
Eyes	0.23		0.04	0.06	1.24	0.60	1.66	1.70	2.02	1.34	1.34
Integument		5.28	1.69	0.86	10.20	5.89	7.69	11.37	13.73	10.25	10.51
Integument flesh (aliquot)		—	0.01	0.01	—	0.05	—	—	—	—	0.065
Integument scales (aliquot)		—	0.02	0.02	—	0.11	—	—	—	—	0.091
Gonad			0.09	0.47		0.08	—	0.004	0.03	0.023	0.020
Kidney	2.40		0.08	0.16	0.22	0.09	0.06	0.027	0.07	0.035	0.022
Light muscle			3.23	8.74	4.19	10.01	12.84	3.94	5.26	5.69	5.79
Dark muscle	16.23		0.10	0.86	5.25	0.70	0.72	0.48	0.47	0.63	0.95

¹ EY = *Euthynnus yailo*.

² CH = *Coryphaena hippurus*.

³ NM = *Neothunnus macropterus*.

We do not interpret the departures from a smooth curve for any one organ to indicate a sequential pattern. In other words, a rise in the radioactivity of one organ and the fall of radioactivity in another are not necessarily linked by way of precursor relations. Each point on the graph represents a single fish, and individual differences can most likely account for the small deviations of the curves.

In order to study the sequential pattern of strontium metabolism, a much larger group of fish would have to be used, particularly since it is known that there is a very large difference in the time a food bolus remains in a fish as compared with another fish of the same species living in the same tank.

The rank order of radioactivity in the organ systems of these fishes is: skeleton, gills, integument, muscle and viscera. It is interesting to note that the dark muscle, which has a better supply of blood, has less radioactivity/gram ash than has the light muscle. Similarly, the "specific activity" of the gills, that is, the counts/minute/mg. ash, was considerably higher than that of the axial skeleton. Goldberg (personal communication) has analyzed yellowfin tuna for various metals, and found that the gill arches and filaments had considerably more strontium in them than had

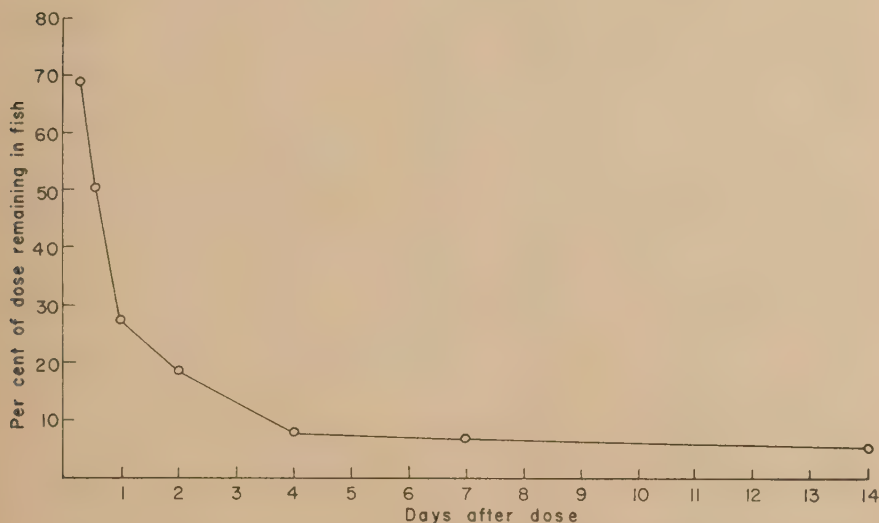


FIGURE 3. The decrease of ingested Sr^{90} in *Tilapia mossambica* as a function of time.

the bones. His values for strontium in the gills would therefore be a minimum value, since any flesh adhering to the sample would tend to dilute the strontium concentration. The main chemical difference between the gill arches and the remaining skeletal tissue is the presence of cartilage in the gill rakers. In our own work, and in the work of others (Jones and Copp, 1951), there is a suggestion that cartilage may have a greater capacity to exchange ionic calcium for strontium than has bone. For example, we have found a higher "specific activity" in the eye, which has cartilaginous ossicles, than we have found in skeletal bone. Moreover, Jones and Copp found that the uptake of strontium by the skeleton is more rapid in young rats than it is in adults. It is possible that the explanation of these differences might lie with an increased amount of Sr^{++} binding by the protein of the cartilage as compared to that bound by the protein of calcified bones. Perhaps differences in the amount of blood supplied to ossified and cartilaginous tissue, or some other properties of cartilage may also be involved.

TABLE II

Percentage of total radioactivity recovered in various organs of *Tilapia mossambica*.
(Each horizontal column represents an individual fish given a dose of 20 μ c)

Duration	Tissue					
	Integument	Eyes	Visceral organs	Gills	Muscle	Skeleton
2 hr.	10.58	0.26	31.88	28.02	9.44	19.81
	1.73	0.08	88.01	1.43	0.83	7.92
4 hr.	12.54	0.36	28.64	23.50	6.45	28.52
	0.32	0.07	65.81	11.34	10.88	11.58
	1.70	0.29	24.41	36.18	6.09	31.34
8 hr.	10.64	1.38	44.50	6.90	3.72	32.85
	8.01	0.24	44.40	15.83	5.46	26.06
	19.66	1.62	11.99	17.10	1.74	47.88
12 hr.	23.07	0.24	42.34	3.65	7.61	23.08
	4.63	1.26	78.36	1.95	1.61	12.19
	7.86	0.67	40.92	8.94	4.26	37.36
24 hr.	25.67	0.32	1.45	9.43	8.96	54.18
	24.93	0.36	1.60	8.60	3.52	60.99
	28.31	0.53	3.57	8.74	4.82	54.03
48 hr.	22.67	0.31	0.62	4.81	1.62	69.97
	5.79	0.83	3.32	14.35	7.39	68.32
	26.48	0.29	1.76	8.40	2.30	60.77
4 days	23.10	0.16	0.40	5.99	2.17	68.17
	26.71	0.27	0.64	8.08	2.38	61.92
	23.63	0.17	0.93	8.20	3.35	63.72
7 days	21.88	0.22	0.97	8.02	2.26	66.65
	20.84	0.21	0.57	8.28	1.92	68.18
14 days	31.42	0.24	0.17	8.92	1.97	56.73
	29.63	0.41	1.10	10.06	2.10	56.69
	20.39	0.22	0.51	8.07	1.24	69.57

B. Ingestion of Sr^{90} by *Tilapia*

Figure 3 shows that the rate of excretion of Sr^{90} by *Tilapia* is much slower than that by the pelagic fishes. About 50 per cent is still present after one day, and the time required to reach a more or less constant level is about four days. The amount

which persists is also larger than that observed with the pelagic fishes, although the variability among the *Tilapia* was fairly large. The *Tilapia* used in these experiments were fed the Sr^{89} in gelatine capsules containing cracker crumbs. Occasionally crumbs were observed in the carboys used to hold three of the experimental fish, and therefore the true dose could not be ascertained. The incorporation of the isotope in gelatine for the later experiments has apparently obviated this difficulty.

Table II presents the data concerning the percentage of the total radioactivity recovered in the various organs and tissues. Figure 4 is a graph of this information except that the ordinate is given in microcuries/gram fresh weight of fish.

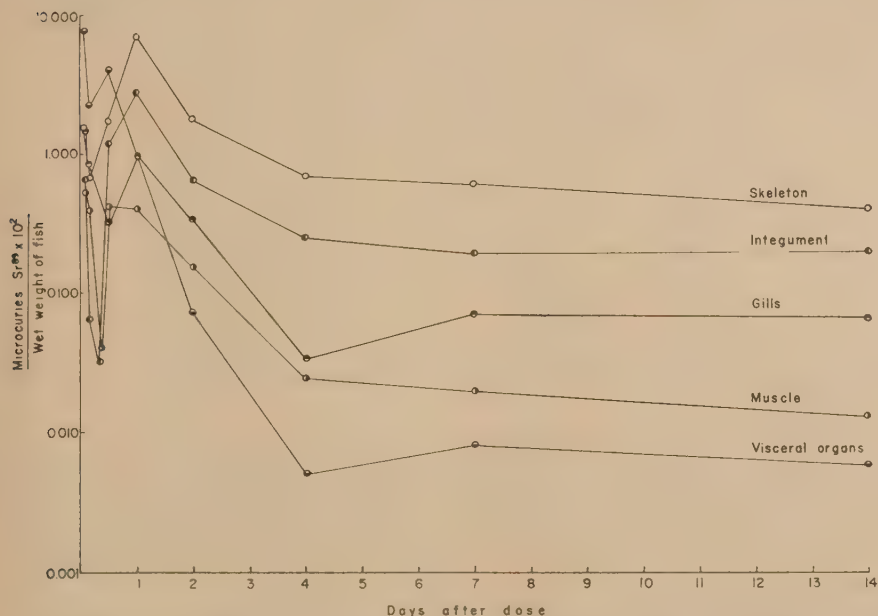


FIGURE 4. The distribution of a single ingestion of Sr^{89} in organs and tissues of *Tilapia mossambica* as a function of time.

The structural tissues account for the bulk of the radioactivity where approximately 90–95 per cent of the activity is present in both *Tilapia* and the pelagic fishes. Roughly, about 60 per cent is accounted for by the skeleton, 30 per cent by the integument, 10 per cent by the gills, 2 per cent by the muscle, and 1 per cent by the viscera. A larger percentage of radioactivity is found in the integument of *Tilapia* than in the integument of the other fishes, probably because a larger percentage of the body weight of this species is due to the large scales. The percentage of the total radioactivity in *Tilapia* was found to decrease in the following order: skeleton, integument, gills, muscle and viscera. The order in the pelagic fishes studied was skeleton, gills, integument, muscle and viscera.

C. The ingestion of Sr^{89} by aholehole

Five aholehole were each fed $48 \mu\text{c}$ of Sr^{89} in gelatine capsules and kept in running sea water 24 hours before killing. The entire fish was then dried and ashed, and Table III shows that the results are much more reproducible than they were using *Tilapia*. After 24 hours the latter fish retained approximately the same percentage of the dose as did the aholehole, but the range was between 2 and 20. No further experiments were conducted with aholehole at this time, but because of their apparent superiority as a laboratory animal we plan to use them in experiments which will be reported at a later date.

Although we have completed some experiments on the repetitive feeding of Sr^{89} , the uncertainty of the exact dose in some instances, and the excessive range of retention by *Tilapia* during short periods have caused us to omit these data here. The results of such experiments on other fish will be reported at a later date.

TABLE III
Percentage of Sr^{89} retained by aholehole 24 hours after ingestion

Fish	Per cent of dose
1	10.43
2	7.42
3	9.16
4	5.70
5	7.97
Aver.	8.13

*D. The uptake and accumulation of Sr^{89} injected intramuscularly into tuna and *Tilapia**

Because our results showed that the biological half-life³ of strontium in fish muscle fell in the same range as that found for the bones and integument, rather than with the soft tissues as was expected, additional experiments were devised to study the retention of Sr by muscle. These experiments also enabled us to study the metabolism of radiostrontium which was introduced by a method other than feeding.

A yellowfin tuna was injected with $288 \mu\text{c}$ of Sr^{89} at the base of the pectoral fin. The fish was killed and analyzed after it had been in running sea water for 19 hours. A comparison of the percentage of Sr^{89} recovered in the organs and tissues of a tuna which received the isotope by injection with that of a tuna receiving an oral dose (Table IV) shows that the digestive organs of the latter were relatively more radioactive than were the corresponding organs of the injected fish. This result is perhaps to be expected, but there are several other outstanding differences in the distribution of the isotope within this time period. The muscle tissue of the fish receiving the injection had almost three times the percentage of Sr^{89} as had the muscle of the fish receiving the radioisotope orally. The gills of the former, on the other hand, had only about half the percentage of Sr^{89} as had the orally dosed

³ We define the term "biological half-life" in this paper to mean the time required for half the labelled strontium to be removed from the tissue or animal in question, exclusive of radioactive decay.

fish. The percentage of radioactivity in the integument and the skeleton of both fish was about the same, and it is not possible to state whether or not the differences found in the remaining organs are significant.

The fact that such a large percentage of the Sr^{89} was retained by the muscle suggested that it might be informative to study this process over a longer period of time. Thus, *Tilapia* were injected intramuscularly between the caudal and anal fin with $\text{Sr}^{89} \text{Cl}_2$ neutralized to about pH 6. The fish were kept in aerated, but not circulating, sea water for the first 24 hours, during which time samples of the water in the aquaria were removed. After 24 hours the fish were put in running sea water and removed at intervals. Figure 5 shows that the radiostrontium was rapidly excreted for about the first twelve hours, and that the rate decreased thereafter.

TABLE IV
A comparison of the percentage of Sr^{89} recovered in the organs and tissues of tuna related to the route of administration

Tissue	Oral ¹	Injected ²
Integument	7.69	7.15
Gill bones	{ 30.61 }	15.25
Gill flesh		1.81
Head, operculum	18.33	14.41
Appendicular skeleton	23.69	23.25
Light muscle	12.84	33.24
Dark muscle	0.72	1.51
Foregut	0.20	0.11
Midgut	0.65	0.36
Hindgut	0.15	0.07
Kidney/gonad	0.06	0.20
Heart	0.05	0.04
Caecum	0.34	0.16
Liver	0.15	0.13
Spleen	0.03	0.02
Gall bladder	0.03	0.37
Blood	2.73	1.79

¹ Skipjack, duration 24 hours.

² Yellowfin, duration 19 hours.

An analysis of the percentage of the dose retained by the fish confirmed the fact that after 24 hours comparatively little strontium was excreted, and that most of the strontium remaining was held by the fish for the duration of the experiment. These results are shown graphically in Figure 6. The points on the graph represent the average of three fish. The greater retention of the five-day fish as compared to the one-day fish can be ascribed to individual variation. The range of retention between the one- and the 21-day fish is of the same order of magnitude as the range of retention at any single time interval. In other words, the curve, neglecting individual differences, is very likely parallel to the abscissa.

The internal distribution of the injected Sr^{89} requires longer to reach a "levelling-off" than does Sr^{89} given orally (Fig. 7). In the former instance, the time required is about one week, whereas in the latter instance the "levelling" occurs within two days. In both situations, however, the percentage of the total radioactivity retained by each of the organ systems is the same.

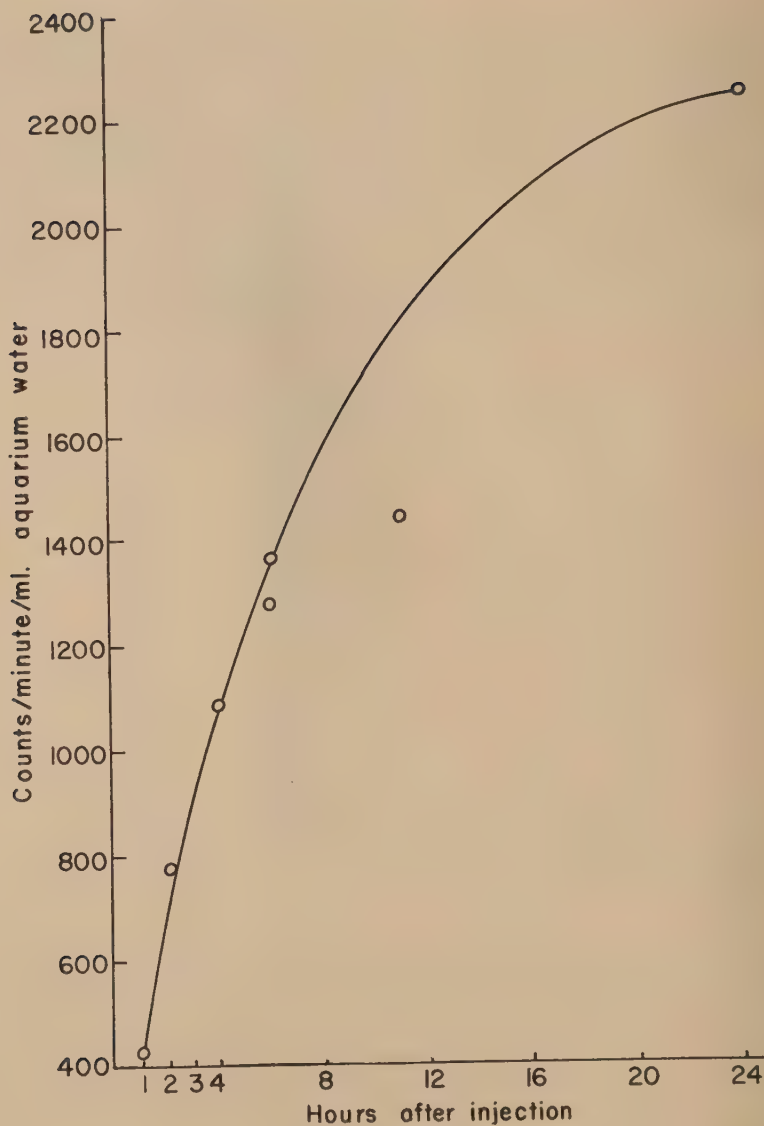


FIGURE 5. The rate of excretion of Sr^{89} injected intramuscularly into *Tilapia mossambica*.

The aquaria used in these experiments were inverted five-gallon carboys with the bottoms removed. Feces and other solid material thus settled to the neck of the carboy and could be removed through glass tubing which just penetrated the rubber stopper. In this way the feces were removed from the tanks six times during the first 24 hours at each sampling of the tank water. The average total



FIGURE 6. The continuing retention of Sr^{89} injected intramuscularly into *Tilapia mossambica*.

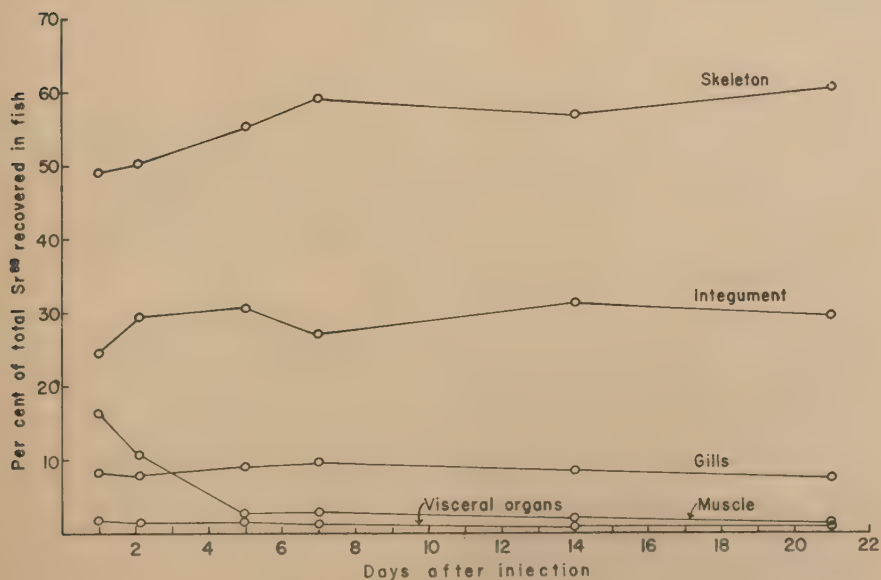


FIGURE 7. The internal distribution of Sr^{89} injected intramuscularly into *Tilapia mossambica*.

Sr^{89} recovered in the feces was 0.35 per cent of the dose at 24 hours, but the amount of leaching is unfortunately unknown.

The injected fish retained a much greater percentage of the dose than did the fish which received the strontium orally. These results suggest that the injected Sr^{89} was actually absorbed to a greater extent, and that the absorption of strontium through the gut is not efficient. Slow, continuous diffusion from the site of injection may also allow a larger amount to become incorporated into the various tissues. If the rate of blood supply to the muscles is less than that to the visceral organs, one might expect the muscle to retain the strontium for a comparatively longer period. The fact that the dark muscle of tuna retained much less strontium than did the light muscle (Table I), and the fact that the dark muscle is better supplied with blood than is the light muscle, suggest that the degree of vascularization is of some importance. One might therefore reasonably expect the cartilaginous tissues, such as the gill rakers and gill rays, to retain the strontium for longer periods than does the bone which is better supplied with capillaries.

Although the amount of strontium in tuna muscles and visceral organs is of the same order of magnitude (Goldberg, personal communication), some specific binding of strontium may occur with muscle protein which does not occur with the proteins of the visceral organs. Further, the very long biological half-life of strontium in the muscle suggests that fish muscle may not be in such a "dynamic state" as one ordinarily assumes according to the researches of Schoenheimer and his associates (Schoenheimer, 1942). Moreover, there is evidence that mammalian muscle protein has a very much slower turnover rate than has the proteins of the visceral organs (Tarver and Schmidt, 1942). Therefore, the slow turnover of strontium in the fish muscle may be only a reflection of the slow turnover of muscle in general.

E. The uptake and accumulation of Sr^{89} in solution by *Tilapia*

Because the pattern of distribution of Sr^{89} in the tissues and organs of several species of fish appears to be similar, both when the isotope was given orally and by injection, one might extrapolate and conclude that regardless of the mode of entry, the internal distribution of Sr^{89} ultimately would be the same. However, to secure more information on this point, and to ascertain whether or not fish could take up strontium directly from the sea water, a situation which is possible in nature, the experiments described below were carried out.

Six *Tilapia* were put into each of four tanks containing 20 liters of filtered sea water and 1744 μC of Sr^{89} . The water was aerated during the experiment, but the fish were not fed. The total amount of Sr^{89} available during the experiment can be considered constant, since even at 21 days, the total Sr^{89} removed by six fish in a tank was less than one per cent of the available dose.

Figure 8 shows the rate of uptake from solution in terms of microcuries of Sr^{89} /gram fresh weight of fish. The rate slows down considerably after about a week, but uptake is apparently still continuing. The ordinate on the right indicates that within 21 days, the ratio of internal Sr^{89} to external Sr^{89} is still less than one.

The internal distribution of the Sr^{89} taken up from solution is shown in Figure 9. The Sr^{89} found in the skeleton is about 40 per cent as compared with a value close to 60 per cent when the strontium is fed or injected. The amount found in

the integument in all cases is about the same, and the gills and muscles show little variation. The amount found in the visceral organs, however, is markedly different. The individual organs were not ashed and counted separately because of their very small size, so it is not possible to state in what organ or organs the very large percentage of Sr^{89} was located.

Since marine fish in general swallow more water than do fresh water fish to maintain proper osmotic balance, it is possible that the principal route of entry of the isotope in solution is by way of the gut. However, our direct feeding experi-

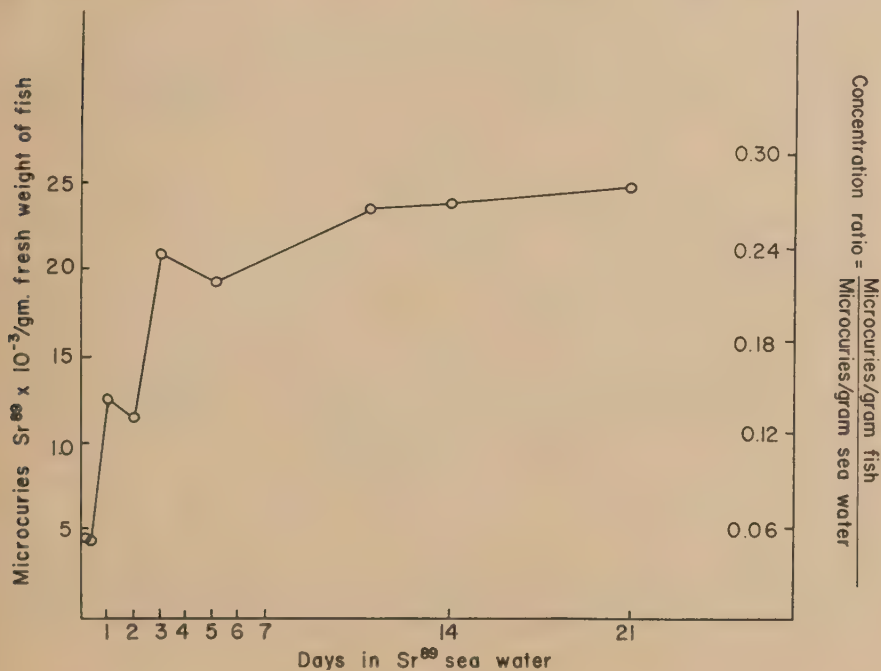


FIGURE 8. The uptake of Sr^{89} in solution by *Tilapia mossambica*, expressed as the concentration ratio.

ments with a variety of fishes indicate that strontium is rapidly eliminated from all the visceral organs. How is it, then, that so much strontium remains in the visceral organs when the fish is immersed in the isotope? A probable explanation is that the fish is being fed the isotope continually, in effect, every time it swallows. Since the concentration of Sr^{89} was found to be higher in the sea water than in the fish, only a small amount of sea water present in the gut would account for the large percentage of total Sr^{89} which was found in the visceral organs. The concentration of Sr^{89} in the sea water was $8.7 \times 10^{-2} \mu\text{c}/\text{ml}$. Assuming arbitrarily that 50 per cent of the total Sr^{89} of the fish was in the visceral organs (Fig. 9), this amount equals about $12 \times 10^{-3} \mu\text{c}/\text{gram fresh weight of the organs}$. If only from 0.1–0.2 ml. of sea water was present in the gut, this would account for the radioactivity

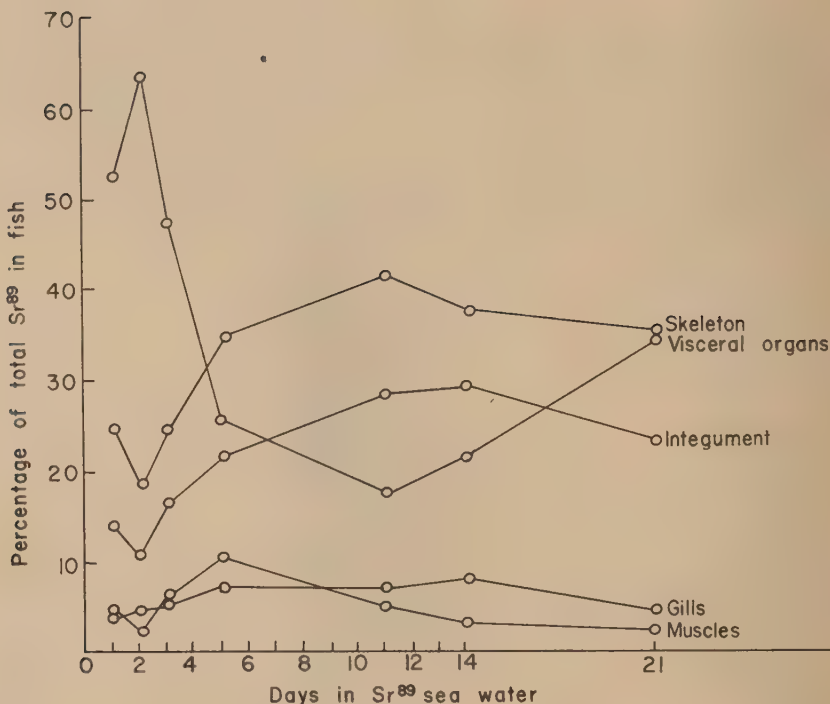


FIGURE 9. The internal distribution of Sr^{89} taken up by *Tilapia mossambica* from sea water.

found. What is important, then, is the rank order of radioactivity in the various organs and systems. Excluding the visceral organs for the reasons given above, it is seen that the other organ systems studied fall in the same rank order regardless of the mode of entry of the radiostrontium.

SUMMARY

1. The ingestion of Sr^{89} by large pelagic fishes results in the excretion of most of the isotope in a few hours. The small percentage remaining after one day persisted for the 27 days of the experiment. The strontium is rapidly eliminated from the visceral organs and tissues, but the structural tissues, including the bones, gills, integument and muscle, maintain their strontium level more or less constant. The turnover of strontium in these latter tissues is therefore slow.

2. Dark muscle, which has a better blood supply than light muscle, retains less Sr^{89} . Similarly, bone, which is better supplied with blood than is cartilage, retains less Sr^{89} than the gill arches or the cartilaginous eye ossicles.

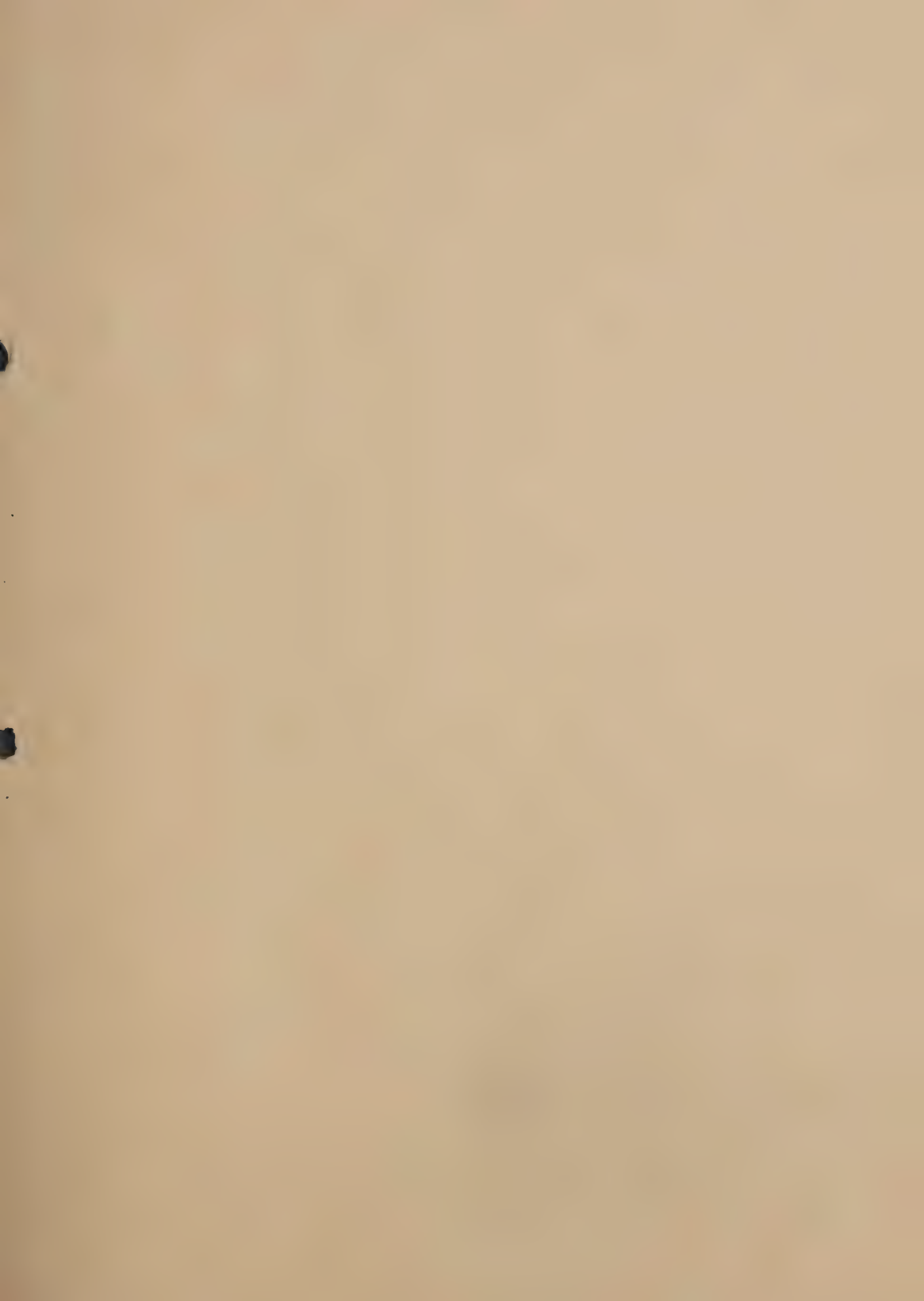
3. The excretion of Sr^{89} by *Tilapia mossambica* is much slower than it is by the pelagic fishes. The percentage of the dose retained is somewhat larger, and most of the radioactivity is found in the structural tissues.

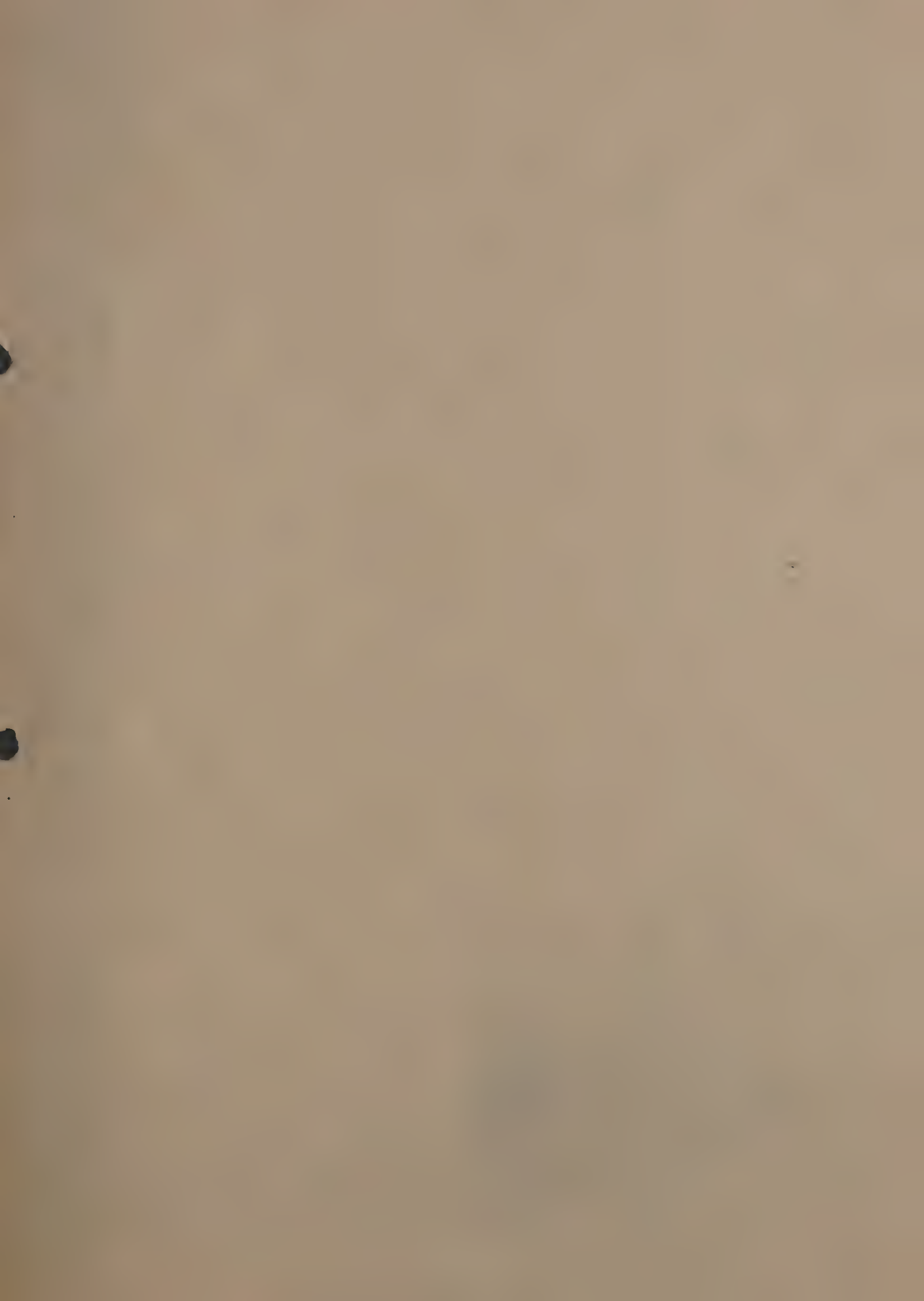
4. About three times as much Sr^{89} was found in the muscle of an injected tuna as compared with another fish receiving the isotope orally. The gills of the former fish had only about half the activity found in the latter. From 60–70 per cent of the dose injected into *Tilapia* muscle was retained by these fish for 14 days. The long biological half-life of Sr^{89} in fish muscle is contributing evidence for the slow turnover of muscle tissue in comparison with such tissues as liver or kidney.

5. *Tilapia* were able to concentrate Sr^{89} directly from the sea water, although the ratio of Sr^{89} in the fish to the Sr^{89} in an equal weight of sea water was only about 0.3 after three weeks. Except for the visceral organs, the rank order of the retention of radioactivity in the various tissues is skeleton, integument, gills and muscle. This is the same distribution as was observed after oral administration of Sr^{89} . Because marine fish swallow water continually, a small amount of water in the gut might account for the relatively large percentage of radioactivity found in the viscera.

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Reprinted from BIOLOGICAL BULLETIN, Vol. 111, No. 3, 352-357, December, 1956
Printed in U. S. A.

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A study of the metabolism of radioyttrium is important for two reasons: first, yttrium⁹⁰ occurs as the daughter of long-lived strontium⁹⁰, an element which has considerable interest from the standpoint of public health; and second, yttrium⁹¹ occurs as a direct fission product to the extent of about four per cent of the total radioactivity present in a fission product mixture one year old. Fission products are being introduced into the seas to a small extent as a result of fall-out, and also from nuclear reactor plants located near the seaboard. The latter situation now occurs in the Irish Sea near Harwell, and more activity of this type may occur as reactor plants increase in number. Spooner (1949), in a noteworthy study on the metabolism of radioyttrium by marine algae, showed that this element was capable of being concentrated by certain algae, and thus stimulated the interest of marine biologists to learn more about the metabolism of the nuclide of mass⁹⁰.

Because we had begun experiments on the metabolism of strontium⁸⁹ and strontium⁹⁰, both of which contain a certain amount of yttrium⁹⁰, we were interested in comparing the metabolism of these two elements in marine fish. Although the ratio of Sr⁹⁰: Y⁹⁰ in an equilibrium mixture is about 3000:1, it was conceivable that some of the results we obtained might have come from the small amount of yttrium present.

In a number of instances the concentration of certain elements is sometimes greater within a marine organism than it is in the surrounding sea water (Noddack and Noddack, 1939; Vinogradov, 1953). For example, one cannot predict, let alone explain, why one species of green algae will accumulate yttrium almost exclusively from a mixture of strontium and yttrium, while another accumulates strontium exclusively. Thus, Rice (1956) reports that *Carteria* sp. takes up 100 per cent of its radioactivity from the strontium in a Sr⁹⁰-Y⁹⁰ mixture, but *Chlorella* sp., which is also a member of the Chlorophyceae, has 95 per cent of its radioactivity in the form of yttrium. Such tremendous differences in accumulation cannot be explained on the basis of size, that is, surface per gram protoplasm. Rather, the explanation is more likely to be one involving the chemical nature of the surfaces among the different algae. Because closely related algae are able to concentrate one element more than another, it is not unreasonable to suspect that one organ of a fish might have a greater avidity for yttrium than it has for strontium. Unfor-

¹ This work was carried out with the aid of Contract No. AT(04-3)-56 between the Atomic Energy Commission and the University of Hawaii.

² Contribution No. 83, Hawaii Marine Laboratory, University of Hawaii.

unately, the small size of the fish used in these experiments did not permit us to separate the visceral organs in detail, so that we can only report the amount of radioactivity found in the integument, skeleton, gills, muscle, and in the combined visceral organs.

MATERIALS AND METHODS

Yttrium⁹¹, obtained from Oak Ridge, was incorporated into a two per cent gelatine solution, and 0.5 ml. was drawn up into a piece of Tygon tubing of small diameter. When the solution solidified, it was extruded directly into the fish's stomach with the aid of a syringe. The dose was 5.5 microcuries. The fish used were *Tilapia mossambica*, each of which weighed about 100 grams. After the radioyttrium was administered, three fish were put into a single carboy with 20 liters of sea water which had been filtered through a No. 4 Mandler filter. Four carboys were used for the four time intervals of 1, 2, 4 and 14 days. The water was aerated, but the fish were not fed. Twenty-four hours after the administration of the yttrium, the fish were put in tanks with running sea water where they were kept until killed rapidly by flooding the gill chamber with ether. After removing the eyes and the visceral organs, the remainder of the fish was put in a pressure cooker which was brought to 20 pounds pressure and then allowed to cool. This process allows the skeleton and integument to be separated easily from the muscle with no leaching of the radioisotope. The separated organs and tissues were dried and ashed at about 550° C. The ash was spread on aluminum planchettes with the aid of a wetting agent, dried under infra-red lamps, and counted with a G-M tube and a conventional scaler for a minimum of 2560 counts. Yttrium⁹¹ has a maximum energy of 1.5 Mev. No corrections were made for the self-absorption which was very small at the densities employed ($< 6 \text{ mg./cm.}^2$). An aliquot of the dose was counted for reference and to correct for decay.

RESULTS

Figure 1 shows that radioyttrium is very rapidly excreted by *Tilapia*. After two days, the fishes retained only about two per cent of the ingested dose (1.6 ± 0.5). In a similar experiment, the average amount of Sr⁸⁹ retained by *Tilapia* after two days was 20 per cent, and even after 14 days, the average retention was about six per cent (Boroughs, Townsley and Hiatt, 1956). The actual absorbed dose may be something less than these values, because marine fishes swallow water in order to maintain their osmotic balance. A small amount of recently swallowed water would therefore be trapped in the gut unabsorbed, but contributing to the radioactivity in the visceral organs. Any feces remaining in the gut would also add to the radioactivity of the visceral organs. In both instances, however, the amount would be small.

Figure 2 indicates that most of the yttrium is retained in the viscera. In rats, the liver, kidney and spleen accumulate yttrium (Hamilton, 1948), but our methods did not permit us to localize the accumulation of yttrium in the visceral organs. Future experiments to disclose this are underway. Assuming that all the radioactivity recovered in the 14-day fishes was absorbed (1.3 per cent of the dose), the

viscera retained 43 per cent, the muscle 29 per cent, the skeleton 16 per cent, the integument 8 per cent, and the gills 4 per cent. The large percentage of yttrium accumulated in the fish muscle was wholly unexpected, for in rats 65 per cent of the absorbed dose was found in the bones (Hamilton, 1948).

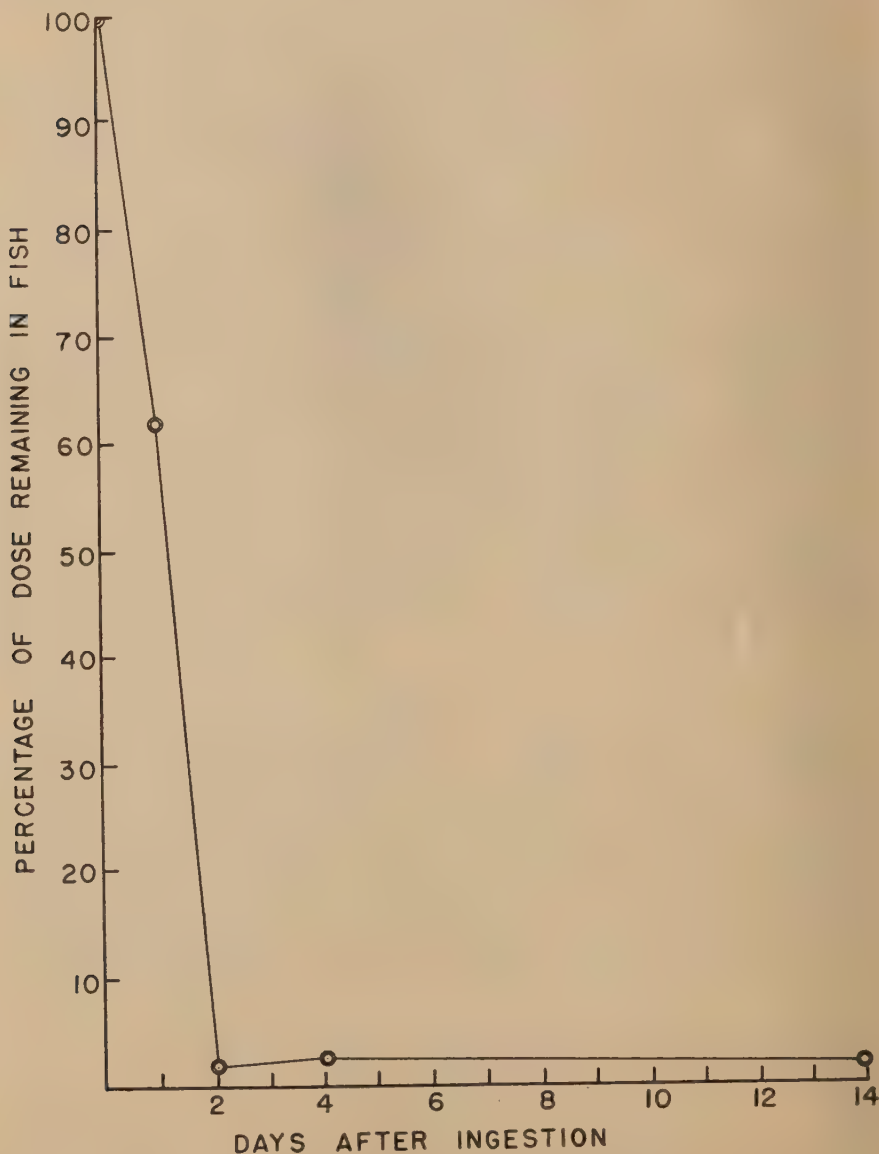


FIGURE 1. The loss of yttrium⁹¹ after ingestion by *Tilapia mossambica*.

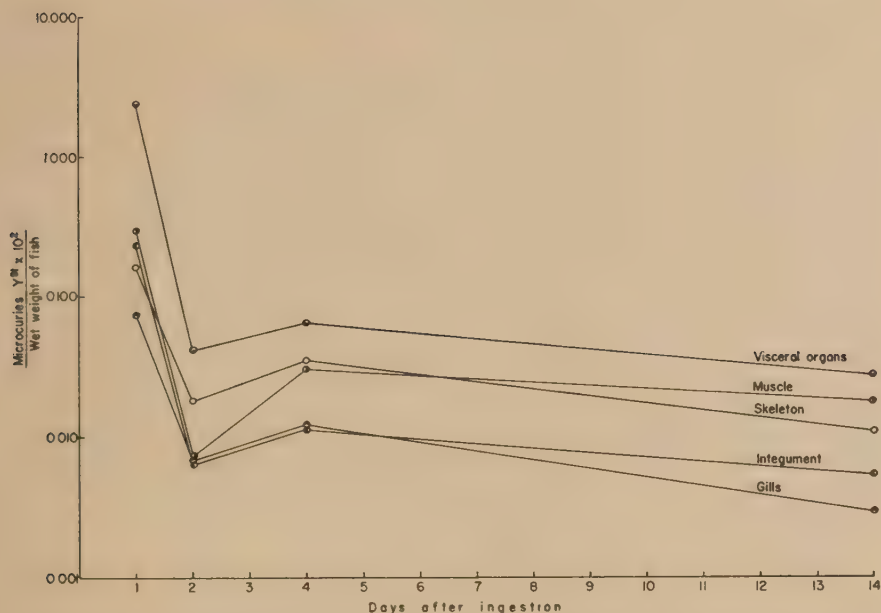


FIGURE 2. The internal distribution of yttrium⁹¹ fed to *Tilapia mossambica* via stomach tube.

DISCUSSION

Similar experiments with radiostrontium (Boroughs, Townsley and Hiatt, 1956) have indicated that in 14 days, *Tilapia* have about 60 per cent of the absorbed dose in the skeleton, 28 per cent in the integument, 9 per cent in the gills, 2 per cent in the muscle, and 1 per cent in the viscera. The rapid excretion of radioyttrium by *Tilapia*, coupled with the different patterns of internal distribution, indicate that the metabolism of strontium and yttrium in this species is markedly different. However, this is not too surprising in view of the difference in chemical behavior between these two elements. Studies on the accumulation of strontium by pelagic fish (Boroughs, Townsley and Hiatt, 1956) showed that this element is rapidly absorbed by all the tissues, but is also rapidly lost from the visceral organs and the blood. Similar experiments with *Tilapia*, a small sluggish fish, were unsatisfactory because of the large variability in the amount of Sr⁸⁹ absorbed over periods up to 24 hours. We therefore made no attempt to follow the pathway of yttrium immediately after ingestion, but very likely yttrium is not actually absorbed to the extent that is strontium. At 24 hours, about 60 per cent of the dose was still in the entire fish, but most of this was in the gut. However, at least 5 per cent of the dose was absorbed by the muscle alone. This is at least 100 times more than the amount absorbed by rats from an oral dose (Hamilton, 1948), and, moreover, represents a minimum value for *Tilapia*.

The maximum percentage of ingested strontium which was recovered in the feces of *Tilapia* during 24 hours was less than 1 per cent. The feces were removed six or seven times during this interval, but some leaching of Sr⁸⁹ may have occurred.

The percentage of Y^{91} recovered in parallel experiments has been as much as 20 per cent of the dose.

If the length of time required for an organ to excrete one-half of its concentration of a particular element is very long (biological half-life), then the effective biological half-life approaches the half-life of the radioisotope involved (radioactive decay). Elements which lodge in mammalian bones appear to have a very long biological half-life. According to Figure 2, however, the biological half-life of yttrium in all the tissues of *Tilapia* is of the order of one month. This value is of course only a guess, and long term experiments will have to be carried out to verify this estimate. In man, the body burden tolerance for Y^{91} is given as about 15 times that of Sr^{90} (N.B.S. Handbook 52), and in both instances the bulk of the radioactivity appears in the skeleton. In one year, the radioactivity owing to Y^{91} would be reduced to a negligible amount because of both excretion and decay, but very little Sr^{90} would be lost in this time. However, in organisms other than man, particularly marine organisms, one year may be a substantial part of their life span, and it is for this reason that we urge that attention be paid to the metabolism of radioactive fission products other than strontium. While strontium may constitute the most serious *direct* health hazard to man, long term effects of other shorter-lived fission products may have significant effects on the shorter-lived biota, and thus ultimately may also prove of importance to man.

There is no evidence that the slight increase in the radioactivity of the oceans has as yet caused any adverse ecological changes. Moreover, there is no evidence that adverse ecological changes will occur even as a result of the introduction of much larger amounts of radioactivity from nuclear reactor plants which are certain to be established within the next decade or so. If the present power requirements of the world are to be met with the aid of atomic energy, it is likely that a sort of steady-state condition will occur with regard to the added radioactivity in the oceans—the result of a balance between the rate of introduction of radioactive wastes, the rate of physical decay, and the rate of biological turnover. It is therefore imperative that marine biologists study in great detail the problems of the uptake and accumulation of fission products, the transfer of these nuclides back and forth among the trophic levels, and the direct, long-term effects of the nuclides in specific regions. Estuaries and the littoral zone will most likely have a higher concentration of radioactivity than the open sea, and it is in these regions that the bulk of the world's marine resources is produced.

SUMMARY

Only about 2 per cent of an ingested dose of yttrium⁹¹ was left in *Tilapia mosambica* after two days. This is much less than the amount of strontium retained by *Tilapia* in similar experiments. About 40 per cent of the radioisotope remaining is found in the visceral organs, but the muscles retain about 30 per cent after 14 days. The skeleton retained less than 20 per cent, the integument about 10 per cent, and the gills 5 per cent. These findings are in marked contrast with those obtained with strontium⁹⁰ in similar experiments. Attention is focused on the fact that yttrium⁹¹ may have little direct effect on man compared with the possible effects of Sr^{90} , but the retention of this and other short-lived fission products in

marine organisms having a brief life span may possibly affect the biota, and thus affect man indirectly.

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